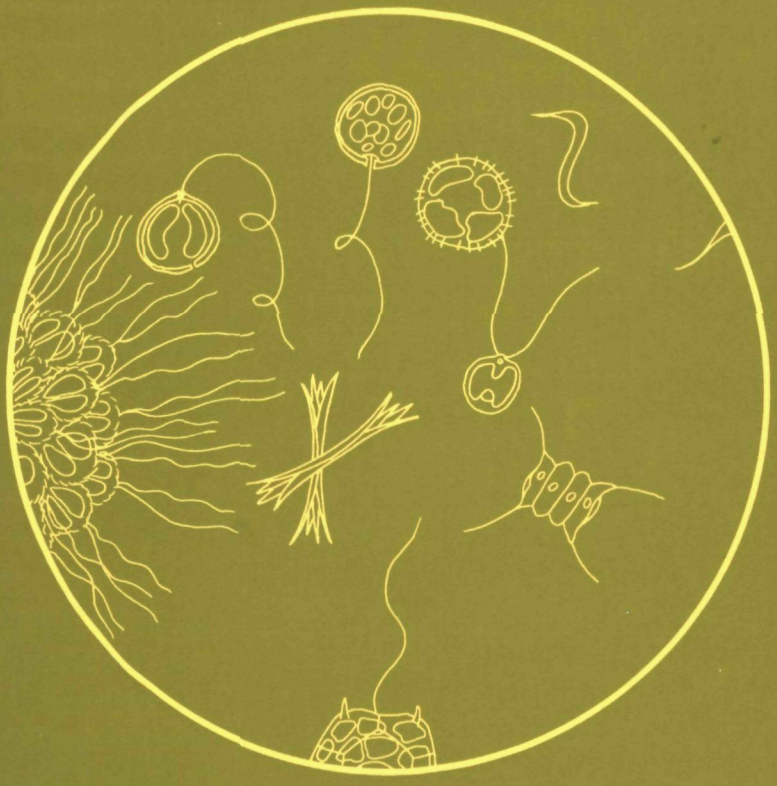
PHYTOPLANKTON STUDIES

IN A NYMPHAEID-DOMINATED SYSTEM



R. M. M. ROIJACKERS

PHYTOPLANKTON STUDIES IN A NYMPHAEID-DOMINATED SYSTEM

with special reference to
the effects of the presence of nymphaeids on
the functioning and structure of the phytoplankton communities

Promotoren: Prof. Dr. C. den Hartog
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PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR IN DE
WISKUNDE EN NATUURWETENSCHAPPEN
AAN DE KATHOLIEKE UNIVERSITEIT TE NIJMEGEN
OP GEZAG VAN DE RECTOR MAGNIFICUS, PROF. DR. J. H. G. I. GIESBERS
VOLGENS HET BESLUIT VAN HET COLLEGE VAN DEKANEN
IN HET OPENBAAR TE VERDEDIGEN
OP MAANDAG 16 DECEMBER 1985
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aan mijn ouders

"groene wolckjens, van de huijsluijden daar omtrent woonende ... honich-douw genoemt"
"kleijne diertgens, daervan eenige waren rontachtig die een weinig grooter waren bestonden uijt een eijront: aen dese laetste heb ick twee beentgens gesien, omtrent het hooft ende aen het achterste van het lichaam twee vinnetgens, andere waren wat langer als eijront, ende dese waren traegh int bewegen en weijnich in getal; dese voorverhaelde diertgens bestonden uijt verscheijde couleuren, als eenige witachtigh ende doorschijnende, andere uijt groene seer glinsterende schibbetgens, ander weder int midden groen en voor en achter wit .... en ick oordeelde dat eenige van dese diertgens meer als duijsentmael kleijnder waren als de kleijnste diertgens die ick tot noch toe op de korst van de kaes, int tarwemeel, in de schimmel ende etc. heb gesien"

ANTONIE VAN LEEUWENHOEK

Passages uit zijn 6e brief aan de Royal Society te Londen (dd. 6 september 1674), waarin voor het eerst in de geschiedenis planktonorganismen uit oppervlaktewater (Berkelse plassen bij Delft) worden beschreven; het betreft waarschijnlijk: *Spirogyra* sp., een Ciliaat en *Euglena viridis*.

Dankwoord

Ik wil iedereen die aan de totstandkoming van dit proefschrift heeft bijgedragen oprecht bedanken.

Contents

1. Introduction

The Netherlands, arisen as the sedimentation delta of the rivers Rhine, Meuse and Scheldt, are known as a largely flat country. A characteristic feature of this country are shallow waters in which sedimentation occurs, leading to peat formation in more acid waters and to a more or less complete decomposition in more alkaline waters. In these waters the succession of macrophytes often takes the following course: (Characeae) → magnopotamids → nymphaeids → helophytes (Segal, 1964). In acid waters eutrophication and saprobic processes lead to an increase in pH and to mineralization of organic material. Both in originally acid and in alkaline waters a sharp increase in the input of inorganic and organic matter eventually leads to an accumulation of organic material (gyttja), and in that case the above-mentioned succession series may take a different course: (Characeae) → magnopotamids → filamentous algae → phytoplankton blooms. In a time in which processes of eutrophication and saprobic processes are greatly enhanced by human activities, the generally existing fear for the loss of many typical shallow waters with their characteristic macrophytes as a result of the general leveling of the - decreased - water quality, necessitates a well-structured management. This kind of management requires a thorough knowledge of the ecosystem as a whole and not only of its constituent structural elements. It is important to know the general trends in all the processes which play a significant role in these surface waters. Since all these processes take place simultaneously and show various interactions, it is difficult to study the elements of these ecosystems separately.

In 1964 Den Hartog & Segal introduced a new classification system for water plant communities, based upon floristic composition, growth and life-form spectrum, physiognomy, stratification and ecology of the vegetation. In their publication the life-form system proposed by Luther (1949) was combined with that of Du Rietz (1921, 1930), which was further elaborated for the rhizophytes and the pleustophytes. Den Hartog & Segal (1964) contend that particular growth forms only occur in specific environments, while (certain) other growth forms predominate in other environments. Ecosystems dominated by macrophytes can be classified according to the growth form of their dominant macrophyte if a

macrophyte is regarded as the main structural element in an aquatic ecosystem.

Since 1973, the Laboratory of Aquatic Ecology of the Catholic University of Nijmegen, The Netherlands, has focussed its attention on the study of some of these macrophyte-dominated ecosystems. Some ecosystems, such as those dominated by *Ruppia* (Verhoeven, 1980) are relatively simple to understand and allow an identification of the major processes which control the development and preservation of these - and other - ecosystems (Van Vierssen and Prins, 1985; Van Vierssen et al., 1985). Other ecosystems are more complex, e.g. the *Zannichellia*-dominated systems (Van Vierssen, 1982), or even extremely complex, e.g. the *Zostera*-dominated systems (Jacobs, 1982a) or the nymphaeid-dominated systems (Van der Velde, 1980; Brock, 1985).

In the study of macrophyte-dominated ecosystems the autecology of the dominating macrophyte is of principal interest, but in addition to this, studies must also be made of the other structural elements of the ecosystem, viz. water, plankton, tripton, macrofauna, associated macrophytes, epiphytes and bottom material, each according to its relative qualitative or quantitative importance for the system as a whole. In fairly simple systems the quantitative aspects will be of particular importance, while in the more complex systems qualitative aspects must also be studied in detail.

A very important ecosystem in the - shallow - Dutch surface waters is the nymphaeid-dominated ecosystem. The study of this system in the Netherlands was initiated by Van der Velde (1980). Nymphaeids are rhizophytes (Luther, 1949) with largely unbranched stems and mainly longly petioled floating leaves, while submerged leaves are often present as well (Den Hartog & Segal, 1964). Nymphaeids occur in a wide range of habitats. They are absent from brackish waters and marine environments. Neither do they occur in the deeper fresh waters, as there is a limit to the possible extension growth of the petioles, which is about 3 m (Van der Voo & Westhoff, 1961). Furthermore, the presence of nymphaeids is largely limited by wind and wave action and by current velocity. Nymphaeids can thus be expected to occur in standing or slow-flowing waters, where we can distinguish two kinds of habitat: a) in the deeper water bodies nymphaeids form a border vegetation, which can be seen as a transition zone between the open water area and the helophyte communi-

ties, and b) in shallow waters (1 - 3m) the entire water body can be colonized by nymphaeids. In many systems both types of habitat can be found (as for instance in the Oude Waal near Nijmegen, The Netherlands).

The study of the nymphaeid-dominated system was planned as an integrated ecosystem study: aspects of the nymphaeid system are studied separately, but also in their interrelations. The nymphaeid plants themselves are considered to constitute the framework of the ecosystem, and all aspects of the system have to be studied in order to understand how the vegetation develops, how it maintains itself, how other organisms interact with it and how the vegetation influences its surroundings and vice versa. At present the nymphaeid project is still at the level of basic research. As the nymphaeids themselves are the main structural elements in the system, most attention has been paid to the study of their seasonal development. Their floral biology and seed production were studied by Van der Velde et al. (1978), Van der Velde & Brock (1980) and Van der Velde & Van der Heijden (1981). Germination in relation to environmental conditions is being studied by Mr. A.J.M. Smits. Most of the studies have concentrated on the steady-state phase in the nymphaeid development, the phase in which the plants are fully grown, production has reached its maximum, but decomposition also occurs, the phase in which floating leaves are present and the ecosystem as a whole reaches its maximum complexity. For this phase, studies have been made of the production of the nymphaeids (Van der Velde et al., 1979; Van der Velde & Peelen-Bexkens, 1983; Brock et al., 1983a), associated macrofauna (Van der Velde, 1978; Lammens & Van der Velde, 1978; Van der Velde, 1979; Brock & Van der Velde, 1983), and decomposition (Jacobs, 1982b; De Lyon et al., 1983; Brock, 1984; Brock et al., 1985).

Among the major autotrophic components in the nymphaeid systems the epiphytes and the phytoplankton have also been described in separate studies. The epiphytes were studied by Mr. E. Delbecque (Delbecque & Chatrou, 1983; Delbecque, 1983). The phytoplankton will be dealt with in the present thesis.

In this thesis an attempt has been made to present a general survey of the structure and dynamics of the (tycho)phytoplankton of a nymphaeid system, as well as of some effects of the presence of nymphaeids upon the functioning and structure of these phytoplankton communities.

The investigations were restricted to one fresh-water body, in which

both kinds of habitat (the deeper waters with a border of nymphaeids and the shallow waters completely occupied by nymphaeids) were present. Chapter 2 deals with the general description of the study area and surroundings.

Chapter 3 essentially concerns methodology and methods and will also deal with the problems associated with the temporal and spatial scales of phytoplankton distribution and the environmental variables.

In chapter 4 the chemical and physical characteristics of the study area will be given.

Chapter 5 gives a survey of previous and preliminary studies of the phytoplankton in the study area. The preliminary studies were carried out in order to obtain a general insight into the distribution of the phytoplankton communities over the entire study area as well as their distribution in time. They also served to characterize the temporal and spatial variation in phytoplankton biomass.

Chapter 6, 7 and 8 deal with the actual study, which was carried out in a shallow part of the study area, in order to allow a comparison between the phytoplankton in open water areas and that in nymphaeid-dominated areas. The main objective of these investigations was to describe the phytoplankton communities and their development in time as regards their species composition, biomass (Chapter 6) and productivity (Chapter 7), as well as to study some of the possible effects of the nymphaeids themselves upon the phytoplankton communities. In order to study the latter aspect, some productivity experiments were carried out, which are described in Chapter 8. Special attention has been given in these three chapters to the importance of the nannophytoplankton for the total phytoplankton community structure and functioning.

An overall picture of the phytoplankton as a component of the nymphaeid-dominated ecosystem in question, in its relation to the biotic and abiotic environment, is presented in Chapter 9.

2. The study area

The research project was carried out in the Oude Waal, an oxbow lake of the river Waal, which is a branch of the river Rhine. The Oude Waal is located in the Ooypolder, near the town of Nijmegen, The Netherlands (fig. 1a).

The town of Nijmegen is situated on a ridge formed by pleistocene glaciers, while the soil of the Ooypolder consists of a 2 - 5 m thick surface layer of holocene river clay on several pleistocene layers of sand and gravel (fig. 2a). This surface layer shows a sedimentation pattern of young river clay deposits laid down by a strongly meandering river

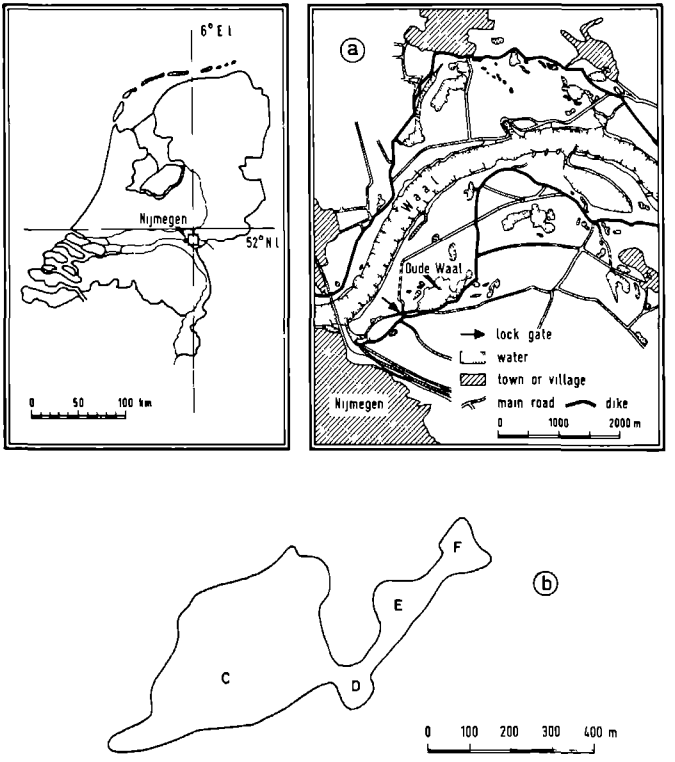


Fig. 1. Map of the study area.
a. The western part of the Ooypolder, in which the Oude Waal is situated. The city of Nijmegen and the river Waal are indicated.
b. The Oude Waal, consisting of the main water body (C) and the three interconnected ponds (D, E and F).

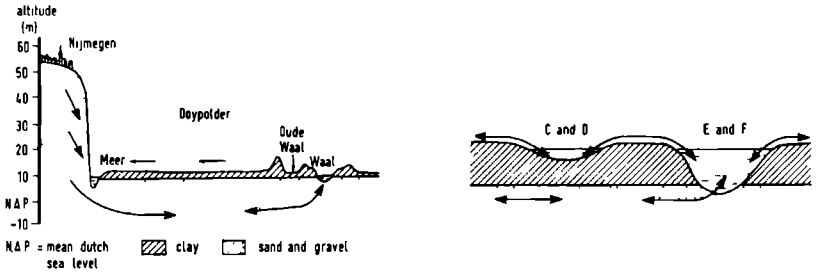


Fig. 2. Diagram of the water movements in the Ooypolder (left) and in the Oude Waal (right).

(Edelman, 1950; Pons, 1957). This pattern consists of riverside ridges, which are rich in sand and thus permeable to water, and of depressions consisting of fine clay and consequently impermeable to water.

The Oude Waal, and the main dike bordering it, are already found on a map dated ca. 1300. After the completion of the embankment in the 14th century the course of the rivers Rhine and Waal was fixed. Only on the river forelands, in which the Oude Waal is also situated, could river deposits settle (wash-over deposits). In subsequent centuries, dike bursts often occurred, and these resulted in deep pits in the landscape caused by the eddying waters. These pits, called 'wielen', could attain a depth of up to 20 m (Leentvaar, 1958). Depending on the course of the newly-built or repaired dike these 'wielen' could be situated on the land-side of the dike, or, as in the case of the two north-eastern ponds of the Oude Waal complex, on its river-side.

The Oude Waal complex consists of the main water body (C) and three interconnected ponds (D, E and F), of which the last two (E and F) originated in dike bursts (F in 1784· E before that time, but the exact year is not known) (fig. 1b). The maximum depths in summer are 1.5, 1.8, 5.5 and 6 m for C, D, E and F respectively. The surface drainage of the region of the Ooypolder, protected by the river-dike against the river Waal, is directed towards the 'Meer', from which the drainage water is pumped into the Waal. Groundwater movements are strongly influenced by the Waal. At high water levels water from the Waal infiltrates into the Ooypolder; at low levels the polder loses groundwater to the river (fig. 2a). The groundwater closely follows the water levels of the river, although with some delay. The Oude Waal itself is connected to the Waal by a ditch in which a lock gate regulates the inflow and outflow of Waal-water (fig. 1a).

Fig. 3 shows bathymetric maps of ponds F and D, the two ponds of the Oude Waal in which the investigations were concentrated. The dotted areas in both maps indicate the nymphaeid-dominated parts. In pond F *Nuphar lutea* (L.) Sm. was clearly dominant, accompanied by some stands of *Nymphaea alba* L. and a small border of *Nymphoides peltata* (Gmel.) O. Kuntze. In pond D *Nymphoides peltata* was the dominating nymphaeid, together with *Nuphar lutea*, whereas *Nymphaea alba* was restricted to a few small stands. The differences between the open water areas (F_1 and D_1) and the nymphaeid-dominated areas (F_2 and D_2) are greater in pond F than in pond D as the differences in depth are greater in pond F. Pond F is more sheltered than pond D. The water masses of D_1 are completely mixed, whereas in F_1 stratification occurs in summer.

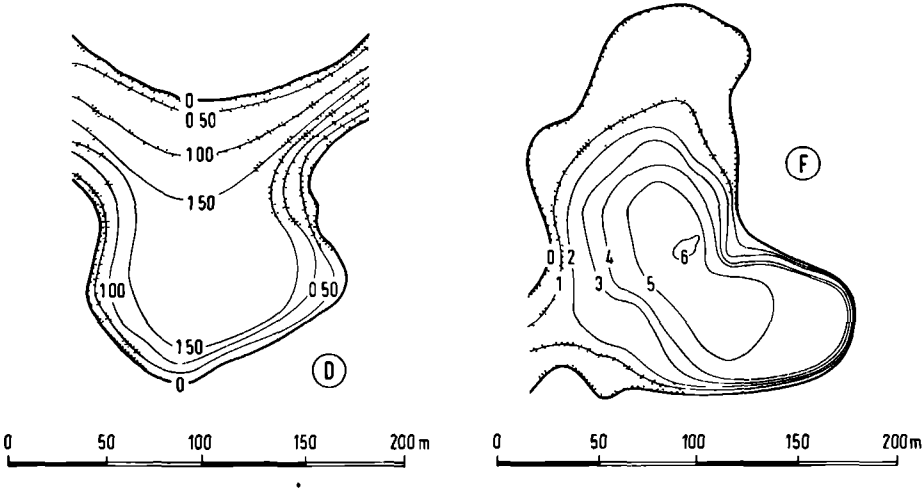


Fig. 3. Bathymetric maps of pond D and pond F.
The figures represent the depths in metres. The dotted areas indicate the areas where the nymphaeids occur (F_2 and D_2); the open areas indicate the open water areas (F_1 and D_1).

3. MATERIALS AND METHODS, WITH CRITICAL REMARKS ON METHODOLOGY

3.1 INTRODUCTION

Ecological investigations inevitably lead to statistical problems (Pielou, 1969; Sournia, 1978; Legendre & Legendre, 1983). In the case of plankton ecology the very first problem to be solved is whether a sample taken from a water body is representative of that water body as a whole or not. Furthermore, if data collected at different times and/or localities are to be compared, one is again forced to use statistical methods. Furthermore there is the problem of the continually changing environment. Hence in this chapter, ample attention will be paid to methodology.

3.1.1. Sampling frequency

The primary objective of the present study was to search for possible effects of the nymphaeids upon the phytoplankton, as regards its structure and functioning. The aim of the study was not to discover these effects in laboratory experiments; instead, an attempt was made to investigate the phytoplankton in its natural environment. Hence, in order to investigate the possible influence of the nymphaeids upon the phytoplankton, it was decided to make a comparison between the phytoplankton in parts of the Oude Waal in which nymphaeids dominated and in parts in which nymphaeids were absent.

The only way to overcome the interference of the variability of environmental circumstances with the results of the study was to increase the sampling frequency. Because of the amount of time involved in the analyses of the samples, sampling is often carried out at monthly, or at the most, fortnightly intervals. The problems arising when one is trying to interpret data based upon monthly samples, as compared to weekly samples, particularly in the light of biomass development, have been discussed and illustrated by Roijackers (1981d). It has become more and more common to sample phytoplankton as frequently as possible, since researchers have become more and more conscious of the rapid changes occurring in phytoplankton communities as a result of the rapid turnover of the organisms themselves (doubling times are often in the range of

0.1 - 6.0 days; cf. Harris, 1980, Round, 1981, and table 25 in this thesis). In the present study, sampling was carried out weekly, assuming that if most species have doubling times of about 3 days in the field, a mixture of several different species will change its composition at a rate which enables the investigator to detect it. Each locality has been sampled during one whole year. This was also useful in that the period in which the above-ground parts of the nymphaeids were absent (November to May) could serve as a blank for the comparison of the nymphaeid-dominated part of the Oude Waal with the open-water part.

3.1.2. Vertical distribution of the phytoplankton

Phytoplankton organisms are not homogeneously distributed over an entire water body, neither horizontally, nor vertically (Hutchinson, 1967; Round, 1981). Depending on physical factors such as water temperature or irradiance the water body can show a vertical inhomogeneity, resulting in a stratification if these factors are stable for a period of time (Ruttner, 1940; Round, 1981). As the main sampling place (pond D of the Oude Waal) was not very deep (about 1.5 m), nor extremely sheltered, a constant mixing of the water masses in the vertical direction was to be expected. Nevertheless this hypothesis was tested at regular intervals during the main investigation period by estimating the chlorophyll-a concentration at four different depths in the open water area of that pond (Table 1).

Table 1. Vertical distribution of chlorophyll-a (µg/l) at sampling site D_1 (open water) in the Oude Waal near Nijmegen.

depth (cm)	23-10-78	20-11-78	09-04-79	18-06-79	01-08-79	22-08-79	12-09-79
10	42.1	20.7	57.7	19.4	28.5	45.6	55.0
50	40.1	20.5	58.2	20.1	28.9	44.5	41.0
100	39.7	21.0	58.0	19.1	29.3	55.9	44.0
150	40.9	20.8	58.3	19.7	27.5	47.7	52.5
mean	40.7±1.1	20.8±0.2	58.1±0.3	19.6±0.4	28.6±0.8	48.4±5.2	48.1±6.7

As can be seen from this table, the phytoplankton biomass was homogeneously distributed over the water column (taking into account the

maximum standard deviation of 10% between two chlorophyll-a estimations, as mentioned in Roijackers, 1981a).

In this study, samples taken from the top layer (50 cm) of the water were used, thus allowing more replicate analyses, which improved the reliability of the results.

3.1.3. Horizontal distribution of the phytoplankton

In the earliest views on the planktonic environment it was taken to be homogeneous and at equilibrium over large scales (Harris, 1980). Hutchinson (1961), however, questioned these views, and wondered how so many species could coexist in such environments. In order to explain this, he emphasized the temporal environmental variability. But this non-equilibrium explanation for the unexpected high species diversity during phytoplankton succession (the 'plankton paradox') could not explain how the requisite number of niches was maintained. He dismissed the occurrence of heterogeneous physical environmental gradients as too transitory a mechanism to yield the required niche diversity. However, evidence is mounting that the plankton is not homogeneously distributed over areas ranging in scale from about 1 cm to 100 km (McAlice, 1970; Powell et al., 1975, Harris, 1980). Significant small-scale spatial heterogeneity characterizes the distribution of environmental properties and species. Observations which show that populations of phytoplankton species are neither uniformly nor randomly distributed suggest that phytoplankton communities are uniquely organized (Margalef, 1967). The existence of such microdistributions leads to the conclusion that the environment, contrary to Hutchinson's view, must be heterogeneous in its physical, chemical and biological properties. Therefore the diversity within a given microhabitat may be low, but when populations are sampled in various habitats and pooled, the diversity may become high. Thus patch size and diversity within a patch vary. Margalef (1967) has pointed out that a fundamental characteristic of the phytoplankton mode is that it is highly subject to diffusion, expansion and natural exploitation.

Since any patches that might exist would be small-scaled and would exist only for a short time, it is impossible to detect them by using standard sampling methods, as these methods involve destruction of the

patch(es) involved (in contrast to non-destructive methods such as in vivo fluorescence: cf. Lorenzen, 1966; Herman & Denman, 1977). This view is confirmed by consulting the plankton lists of earlier investigations in the Oude Waal (see chapter 5) which show a high species diversity, implicating pooling of several patches.

In the present study, the following sampling procedure for the field was chosen. 1-Litre samples were taken from at least 15 spots, distributed at random over the sampling locality, and put together in a large polyethylene container. This container was brought to the laboratory, where subsamples were taken from it for further analyses.

3.2. FIELD PROCEDURES

Samples were taken weekly from two sampling localities in pond F or pond D; the two sampling localities in each pond differed in that one had a luxurious nymphaeid vegetation (F_2, D_2), while the other had no macrophyte vegetation at all (F_1, D_1). The sampling period in pond F was from 9 May 1977 to 24 April 1978, that in pond D from 2 October 1978 to 22 October 1979. Within each locality about 15 1-litre samples were taken at random - using a rowingboat - from a depth of 15 cm. These samples were mixed in a 25-litre polyethylene container.
In addition, the following data were collected each week at a fixed point in each sampling locality.

a. Irradiance was recorded above the water (incident irradiance) and at the following depths: 10 (subsurface) - 50 - 100 - 150 cm at F_2, D_1 and D_2 and at F also at 200 - 250 - 300 - 350 - 400 - 450 - 500 - 550 - 600 cm. Measurements were made with a LiCor Li-185A quantum meter with the appropriate underwater quantum sensor.
   In addition, continuous monitoring of incident irradiance was undertaken. The same quantum meter was placed near the Oude Waal and connected to a TOA ERP-2001A recorder. Irradiance was expressed as $\mu E/m^2.sec$ or $E/m^2.h$ PhAR (Photosynthetically Active Radiation: 400 - 700 nm).
b. Temperature was recorded above the water and at a depth of 15 cm under water, using a mercury thermometer or the thermistor of an oxygen meter. Temperature profiles were recorded using the thermistor of the

oxygen meter at the same depth intervals as those at which the underwater irradiance was measured.

c. pH was recorded by means of a Metrohm E488 pH-meter. This meter was calibrated in the laboratory before each sampling trip.

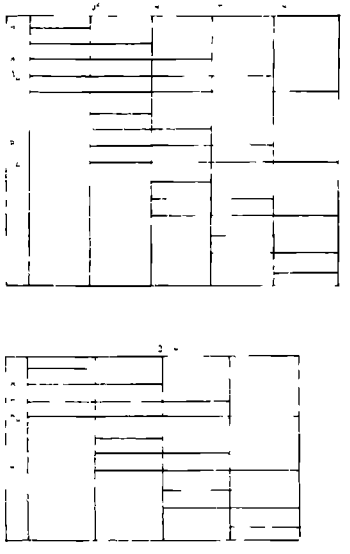
d. Oxygen was measured using a Yellow Springs Instruments YSI-57 oxygen meter. Prior to each sampling trip the probe of this instrument was provided with a fresh membrane and the instrument was calibrated in air-saturated water. The instrument corrects for temperature. Oxygen profiles were recorded at the same depth intervals as those at which underwater irradiance and water temperature were measured.

e. A 1 m^2 wooden frame was used to estimate the percentage of the surface covered by the floating leaves of the nymphaeids. The estimations were carried out in the centre of the nymphaeid stands, i.e. the same places where productivity measurements were also performed.

f. Primary productivity measurements were carried out using the oxygen light and dark bottle technique (Vollenweider, 1969). Incubations were done in sextuplicate, using a wooden frame fixed under water at a depth of 15 cm (fig. 4). The bottles (ca. 125 ml) were filled carefully, eliminating particles larger than 500 µm, and rinsing them three times. Incubation time was about 6 hours (from 10.00 a.m. to 16.00 p.m.). The samples were fixed using the Winkler method (Golterman et al., 1978).

In order to determine to what extent the incubation period was representative of the total light day, experiments similar to those done by Hammer et al. (1973) were conducted. These experiments were carried out four times (August 14. and 22. and September 12. and 26, 1979), both at D_1 and at D_2. In these experiments the period between sunrise and sunset was divided into 4 or 5 periods of equal length. Incubations lasted either for one period or for several successive periods, according to the incubation schemes shown in fig. 5. All productivity data derived from these experiments were standardized towards a standard light day. The productivity data thus obtained were plotted in fig. 6 against a X axis extending from sunrise to sunset. The results of the 4 experiments were averaged. Fig. 6 shows that the phytoplankton productivity exhibits a quick rise both in D_1 and D_2, and then reaches a plateau which is higher for D_1 than for D_2 and eventually falls off slowly. The incubation period was always within the 'plateau' period and included the noon period (Hammer et al., 1973).

Fig. 4. Incubation for the primary productivity experiments. The wooden frame is fixed at a depth of 15 cm under the water surface and the bottles are placed horizontally on the frame. Four polyethylene bottles are used as floaters. The nymphaeids in this photograph are Nymphoides peltata (smaller leaves) and Nuphar lutea (larger leaves).



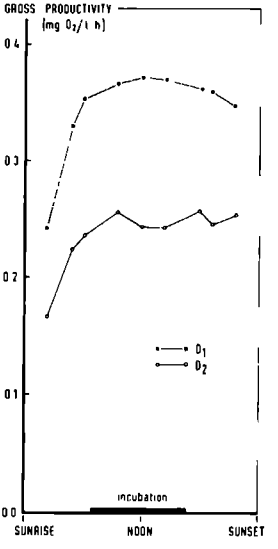


Fig. 5. (left) Incubation schemes for phytoplankton samples for the purpose of primary productivity measurements in pond D of the Oude Waal. Each horizontal line in the scheme represents the duration of the incubation. The above scheme was used on August 14. and 22. 1979; the scheme below was used on September 12. and 26. 1979.

Fig. 6. (right) The phytoplankton primary productivity from sunrise to sunset at the sampling localities D_1 (open water area) and D_2 (nymphaeid-dominated area) of pond D in the Oude Waal.

3.3. LABORATORY PROCEDURES

From the two containers brought to the laboratory each week containing mixed samples from F_1 and F_2 (May 1977 to April 1978) or from D_1 and D_2 (October 1978 to October 1979), subsamples were taken for the following procedures.

a. Identification of the phytoplankton taxa.

One litre was taken from the container, after mixing, and concentrated, using a Sartorius membrane filter (mesh: 3 µm). The concentrated sample was analysed immediately, using a WILD phase-contrast microscope (type M 20 EB). Taxa which could not be identified immediately were photographed until further consultation of the literature might solve the problem. Several important groups of algae (important in terms of biomass as well in terms of number of species) had to be examined separately

using specific methods. The scale-bearing Chrysophytes and Prymnesiophytes were examined by means of transmission and scanning electron microscopes (for further details see Roijackers, 1981b). Diatoms were examined after cleaning the samples by oxidation, which removes the organic compounds from the samples and leaves permanent slides.

b. Quantitative analysis of the phytoplankton organisms during the investigations in pond F.

During the investigations in pond F phytoplankton organisms were not quantified exactly, but a semi-quantitative method was used. The abundance of the organisms was estimated in the samples used for the identification of the taxa by using an abundance scale ranging from 1 to 5 (1 = occasional hit, 1-3 individuals per slide; 2 = 4-10 individuals; 3 = more than 10 individuals, not dominant; 4 = as 3, but dominant; 5 = mass occurrence). Care was taken to follow the same procedure in preparing the samples from each sampling date, in order to produce comparable abundance values from week to week.

c. Enumeration of the phytoplankton organisms during the investigations in pond D.

One litre of water was taken from the container, after mixing, and put in a glass bottle. This subsample was immediately pre-fixed with Lugol's solution (Willén, 1962). The bottle was put away in the dark for two weeks, giving the algae time to settle. After one day the sample was fixed with formaldehyde to a 4% solution. After two weeks of settlement 900 ml of supernatant were siphoned off, resulting in a tenfold concentration of the original samples. Then a 4 ml counting chamber (Geelen, 1969; van Heusden, 1972) was filled, and after settlement of the algae on the bottom of this chamber (2 - 4 hours), the phytoplankton specimens in the sample were counted using a NIKON inverted microscope type MTD.

The results were corrected for the concentration factors used, and were recorded as numbers of individuals per taxon per ml and as numbers of individuals per sample per litre.

d. Determination of the biovolume of the phytoplankton.

The inverted microscope method was used to determine the biovolume of the organisms. Dimensions of the individuals encountered were measured and biovolume was calculated for the different taxa from the mean

dimensions of their cells, assuming that their form corresponds roughly to simple geometrical solids (Findenegg, 1974). The biovolume was calculated in mm^3/l for the taxa and for the total phytoplankton sample.

e. Chlorophyll-a estimations.

A one-litre sample was taken from the container, after mixing, and concentrated over a Whatman GF/C glassfibre filter, which retains particles larger than 1.2 µm in diameter. Extraction of the pigments was performed in hot ethanol (70-75 °C, 80%) and the chlorophyll-a content was estimated according to the method described by Roijackers (1981a) using a Beckman double-beam spectrophotometer model 25. Results were expressed as µg chlorophyll-a/l. These concentrations were corrected for chlorophyll-a breakdown products (Lorenzen, 1967; Moed & Hallegraeff, 1978). All analyses were done in duplicate.

f. Dry weight and ashfree dry weight determinations.

A one-litre sample was taken from the container, after mixing, and concentrated over a Whatman GF/C glassfibre filter. This filter had already been washed and predried at 105 °C for one hour (placed in an aluminium dish) and pre-weighed (w_1). The dish containing the filter plus phytoseston sample was placed in the oven for another hour at 105 °C and weighed again (w_2). Then the dish with the filter plus sample was placed in a muffle-furnace and ashed for 3 hours at 550°C (w_3). The difference between w_2 and w_1 is the dry weight of the seston sample (organic + inorganic substances); the difference between w_3 and w_2 is the ashfree dry weight (organic substances). To correct for deviations arising from possible irregularities in the filter material and/or dishes, dishes with washed glassfibre filters without sample were also dried and ashed and, if necessary, corrections were made in the dry weight and ashfree dry weight of the seston samples. All analyses were done in duplicate.

g. Chemical analyses.

Alkalinity.

Immediately after arrival at the laboratory, 150 ml samples were taken from the container, after careful mixing, for the purpose of determining the alkalinity according to Golterman et al. (1978). Results were recorded in meq/l. All analyses were performed in duplicate.

$P\text{-}PO_4^{3-}$, total-P, $N\text{-}NH_4^+$, $N\text{-}NO_3^-$, $N\text{-}NO_2^-$, total-N, Cl^-, SO_4^{2-}, SiO_3^{2-}.

These elements were all analysed following generally accepted methods, using a Technicon autoanalyser. The samples were analysed in duplicate. All analyses were carried out once a month, which meant that the samples had to be stored. For this purpose the water samples were transferred to 250 ml iodated polyethylene bottles and fixed with $HgCl_2$ to prevent growth of organisms. Only the (50 ml) sample for the Cl^--analyses were not fixed. All samples were kept at -28 °C and were thawed before analysis. The concentrations are given in µmol/l.

Mg^{2+}, Ca^{2+}, Mn^{2+}, Fe^{2+}.

These elements were analysed according to generally accepted methods, using a Beckman Atomic Absorption Spectrophotometer model 1272. The analyses were done in duplicate. Concentrations are given in µmol/l.

Na^+, K^+.

The concentrations of these elements were determined by means of flame emission spectrophotometry. Concentrations are given in µmol/l. All analyses were done in duplicate.

h. Productivity measurements: determination of the oxygen content.

The fixed samples were stored at 4 - 6 °C in the dark awaiting further analysis. The oxygen content was determined titrimetrically using the Winkler method (Golterman et al., 1978). Results are given in mg O_2/l. Respiration is the difference between the oxygen content of the dark bottle after incubation and the initial oxygen content; the net production is the difference between the oxygen content of the light bottle after incubation and the initial oxygen content; the gross production is the difference between the oxygen content of the light bottle and the oxygen content of the dark bottle, both after incubation. The productivity (expressed as mg O_2/l.h) is the production divided by the incubation time. The standard deviation for the 6 replicates was in most cases below 0.05 mg O_2/l.h (15 - 19% of the mean gross productivity) and never higher than 0.08 mg O_2/l.h (24 - 30%).

In figure 7 the field and laboratory procedures have been summarized schematically.

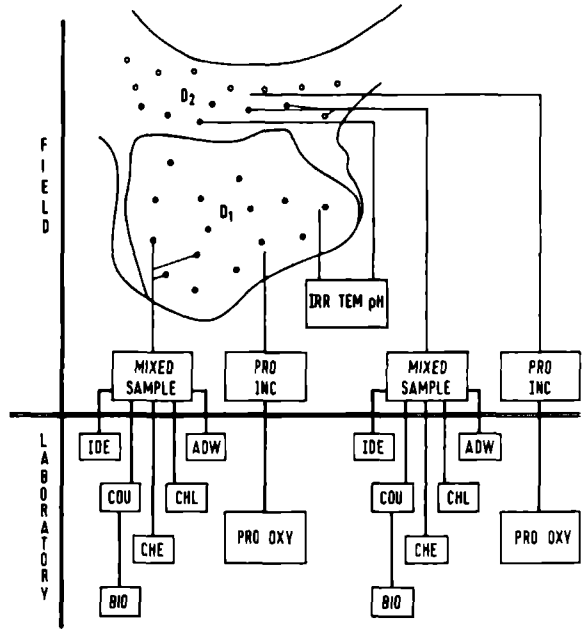


Fig. 7. Schematic summary of analysis procedures used. The 15 open circles in D_2 (nymphaeid-dominated area) and the 15 dots in D_1 (open water area) indicate the subsamples taken. AW = ash-free dry weight; BIO = biovolume; CHE = chemical analyses; CHL = chlorophyll-a; COU = countings; IDE = identifications; IRR = irradiance; pH = pH; PRO INC = productivity incubations; PRO OXY = oxygen determinations of the productivity samples; TEM = temperature.

3.4. ELABORATION OF THE DATA

a. Irradiance.

The continuous measurements of the incident irradiance were recorded graphically. In the graph the surface underneath the curves was determined planimetrically, which - using the appropriate conversion - resulted in the total incident irradiance per day, expressed as E/m^2.day. In order to calculate the production per day, the incident irradiance during the incubation period was needed as well. This was also determined planimetrically from the same curve and expressed as E/m^2.incubation-time.

Irradiance profiles (underwater measurements) were used to calculate the irradiance level at incubation depth (15 cm).

b. Productivity.

In this study gross productivity was used, as this reflects the amount of energy entering the phytoplankton community. In order to

calculate the gross production per day the following formula was used:

$$\text{production per day} = \frac{\text{irradiance per day} \times \text{production per incubation time}}{\text{irradiance per incubation time}}$$

c. The photosynthetic quotient (assimilation number).

For reasons of comparison with other (literature) data and also for the purpose of calculating renewal rates and quantum efficiencies, the production data, expressed as mg O_2/area or mg O_2/volume, were converted to mg C/area or mg C/volume. It is known from the literature that the photosynthetic quotient (PQ = O_2 output/CO_2 uptake by volume) is slightly more than unity. At one time during this study an attempt was made to establish the photosynthetic quotient for a phytoplankton sample from pond D of the Oude Waal. In this particular situation the photosynthetic quotient was found to be 1.24. For the conversion of the production data a PQ = 1.2 (1 mg O_2 = 0.312 mg C) was used (Westlake, 1974).

d. Pigment efficiency.

Hickman (1973, 1976) introduced the 'photosynthetic index' to indicate variations in metabolic rates of naturally occurring algal populations. In order to avoid problems in the use of this rather ill-defined term, I propose to use the term pigment efficiency instead of photosynthetic index, since the index in fact reflects the productivity per unit of chlorophyll-a pigment. Pigment efficiency is the productivity per unit of chlorophyll-a content of a phytoplankton community and is expressed as mg O_2/mg chlorophyll-a.h.

e. Phytoplankton renewal rate and renewal time.

The phytoplankton renewal rate (turnover rate, P/B-ratio) is the rate at which new biomass is fixed per day by a known quantity of biomass; it is expressed as mg C/mg C (biomass).day. If the renewal rate is 0.4/day (or 40%) this means that in 1 day each mg C (biomass) will increase by 0.4 mg C (or in other words, the biomass has increased by 40%).

The phytoplankton renewal rate can be calculated from the pigment efficiency. Instead of gross productivity, net productivity has to be used for the calculations (net productivity is the quantity of energy actually fixed by the phytoplankton as biomass). Productivity has to be converted from mg O_2 to mg C (1 mg O_2 = 0.312 mg C) and the biomass component of the index (chlorophyll-a) must also be converted to mg C

(1 mg chlorophyll-a = 50 mg C (Welch et al., 1978; Ahlgren, 1983)). The phytoplankton renewal time (turnover time, B/P-ratio) is the reverse of the phytoplankton renewal rate and is the time in which the total initial phytoplankton biomass has been renewed or doubled; it is expressed in days.

f. Phytoplankton primary productivity efficiency.

Hickman & Jenkerson (1978) introduced the term phytoplankton primary productivity efficiency. The productivity efficiency is the productivity per unit of chlorophyll-a content of a phytoplankton community per unit of available PhAR-irradiance. In the present study, the productivity efficiency is expressed as mg $O_2.m^2$/mg chlor.-a.E. The productivity efficiency has been calculated for the irradiance level at 15 cm depth instead of for incident irradiance (Hickman & Jenkerson, 1978).

g. Quantum efficiency and quantum yield.

The quantum yield is the efficiency with which absorbed photons of PhAR are converted to photosynthetically stored energy (Tilzer, 1984). Several quantum yield ratios have been proposed in the literature (Bannister, 1974; Tyler, 1975; Dubinsky & Berman, 1976; Haynes & Hammer, 1978; Tilzer, 1984), most of them rather complicated as a result of various correction factors, variables and parameters to be established and used. In the present study, little attention has been paid to these variables and parameters, so efficiency estimates can not be made as accurately as is done in many other studies. In simple terms the quantum efficiency (which is the reverse of the quantum yield) of a phytoplankton community is calculated according to the ratio of photoassimilated carbon to photosynthetically active irradiance available to the phytoplankton (both expressed as cal/m^2.h, both over the same time interval (Haynes & Hammer, 1978)). Primary productivity and irradiance values have to be converted to their caloric equivalents. In the literature, several conversion factors have been used (Winberg, 1971 and Tilzer et al., 1975: 10 cal/mg C; Talling et al., 1973: 12 cal/mg C; Platt & Irwin, 1968, Platt, 1969 and Haynes & Hammer, 1978: 13.3 cal/mg C); in the present study the highest value (13.3 cal/mg C) is used. Because of these differences in conversion, care must be taken in comparing with literature data. Wetzel (1975) therefore advises a deviation of 30% at the most. Irradiance is converted using the relation

1 $E/m^2.h$ = 880 $cal/m^2.min$ (Harris, 1978). Most efficiency values presented in the literature are based on incident irradiance measurements. The values for the Oude Waal, pond D, have been calculated using the irradiance level at a depth of 15 cm, which leads to higher efficiency values than the ones normally reported in the literature (10 - 20% higher, according to Round (1981)).

h. Species composition.

Identified taxa have been collected in tables arranged vertically according to taxonomical position and horizontally according to time.

i. Biovolume of the phytoplankton organisms.

The biovolume of the phytoplankton sample at a given date is put at 100% and the percentual part of the different phyla is calculated and presented graphically.

4. PHYSICO-CHEMICAL CHARACTERISTICS OF THE OUDE WAAL

4.1 INTRODUCTION

As already mentioned in chapter 2, the Oude Waal, situated in the forelands of the river Waal, is greatly influenced by fluctuations in the water level of the Waal. In this chapter attention will be paid to the water level fluctuations in the Oude Waal itself and the effects of these fluctuations upon the water chemistry.

Within the Oude Waal two types of habitat can be distinguished: the shallow parts (C and D) and the deeper ponds (E and F). In summer the main water body (C) is almost completely covered with the floating leaves of nymphaeids, while pond D is only partly covered, pond E has only a border vegetation of nymphaeids and pond F is also partly dominated by nymphaeids. In this chapter physico-chemical characteristics of the deep pond F and the shallow pond D will be given, since a substantial part of the investigations were carried out in these ponds.

4.2. WATER LEVEL FLUCTUATIONS AND CHEMISTRY

The fluctuations in the water level of the Oude Waal are the resultant of a number of factors; climatical ones such as precipitation and evaporation, and hydrological ones such as upwelling via underlying sand layers, leakage through the closed lock gate (see chapter 2, fig. 1a) and inflow over the top of the dike (which is more than 11.35 m above N.A.P. (N.A.P. = mean Dutch sea level)) at very high water levels in the Waal, as well as percolation through the sandy layers and outflow through the opened lock gate. At times of greatly increased water levels the lock gate is closed, which increases the difference in water level between the Oude Waal and the Waal itself. Eventually the water level of the Oude Waal nevertheless rises, as river water percolates, particularly via the deeper ponds E and F, which have a sandy bottom (fig. 2b). At water levels above 11.35 m above N.A.P. the Oude Waal is completely flooded (fig. 8). When the water level of the river drops, the lock gate is opened and excess water will run off. At a water level of 9.10 m above N.A.P. water in the Oude Waal will not be drained off anymore, as this is the lowest possible outflow level of the lock gate. So at water levels lower than 9.10 m

above N.A.P. the water level in the Oude Waal will steady down (fig. 8).

As a result of glacial melting water and heavy rains the water level of the Waal rises once a year (February/March) and occasionally a second time in spring (fig. 8). During the very dry summer of 1976 the main water body of the Oude Waal (C) dried out completely, while ponds D, E and F also showed an extremely low water level. After this dry period precipitation greatly exceeded evaporation (fig. 9) and the water level in the Oude Waal rose, either directly (C and D) or indirectly via the ground water (E and F) (fig. 8).

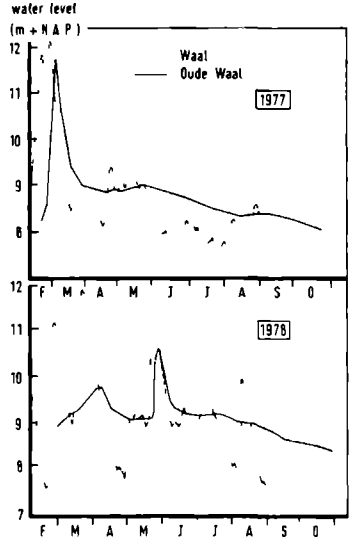


Fig. 8. Water level fluctuations in the Oude Waal (solid line) and in the river Waal (broken line). Above: 1977; Below: 1978.

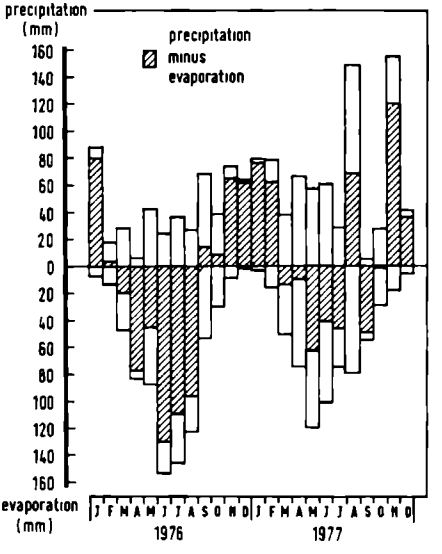


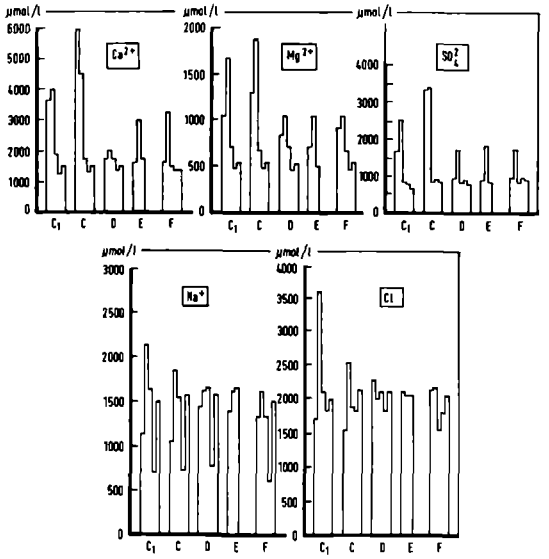
Fig. 9. Precipitation and evaporation in mm in 1976 and 1977. The data (monthly totals) are from the KNMI in De Bilt.

From January 1977 to May 1977 the four parts of the Oude Waal were sampled every month. Table 2 shows the mean concentrations plus standard deviations of some relevant elements in C_1 (the western part of C), C, D, E and F. The influence of the water level fluctuations upon the water chemistry in the Oude Waal can clearly be seen by the much higher standard deviations in the shallow parts of the Oude Waal (C_1, C and D), as compared to the deeper ponds E and F.

Figs. 10 and 11 show the concentrations of some elements for each sampling locality during the period January 1977 to May 1977.

Table 2. Dissolved chemical compounds in the Oude Waal (mean concentrations and standard deviations in µmol/l); period January 1977 to May 1977; sampling localities C_1, C, D, E and F.

	C_1	C	D	E	F
K^+	105 ± 29	127 ± 33	120 ± 38	141 ± 22	114 ± 34
Na^+	2270 ± 780	2230 ± 750	2310 ± 610	2550 ± 230	2110 ± 650
Ca^{2+}	2450 ± 1260	3000 ± 2110	1670 ± 260	2110 ± 770	1810 ± 800
Cl^-	2250 ± 770	1990 ± 380	2050 ± 170	2080 ± 30	1930 ± 260
SO_4^{2-}	1300 ± 770	1840 ± 1380	1090 ± 420	1180 ± 550	1000 ± 410
PO_4^{3-}	0.8 ± 0.6	0.7 ± 0.5	0.7 ± 0.6	1.2 ± 0.5	1.4 ± 1.2
Fe^{2+}	1.3 ± 0.4	0.9 ± 0.5	0.9 ± 0.2	0.7 ± 0.0	0.9 ± 0.4
Mn^{2+}	1.8 ± 2.7	2.7 ± 3.8	1.1 ± 1.3	1.5 ± 1.6	2.6 ± 4.0
Mg^{2+}	880 ± 480	960 ± 590	700 ± 230	880 ± 170	720 ± 250



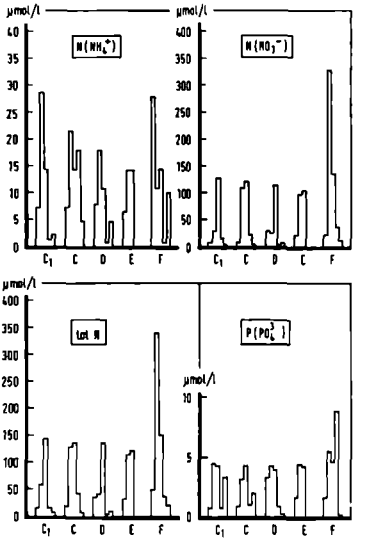


Fig. 10. (left) Concentrations of the major elements in the water of the Oude Waal at sampling localities C_1, C, D, E and F, during the period January to May 1977.
For each sampling locality the five sampling dates are given in the sequence: 10 January, 21 February, 21 March, 18 April and 16 May; sampling locality E was not sampled in April and May.

Fig. 11. (right) Concentrations of the major nutrients in the water of the Oude Waal at sampling localities C_1, C, D, E and F, during the period January to May 1977.
For each sampling locality the five sampling dates are given in the sequence: 10 January, 21 February, 21 March, 18 April and 16 May; sampling locality E was not sampled in April and May.

The fluctuation pattern in the concentration of the conservative ions (Mg^{2+}, Na^{+}, Cl^{-}), but also that of the dynamic ions (Ca^{2+}, NH_4^{+}, SO_4^{2-}, NO_3^{-}, PO_4^{3-}, tot. N) closely follows the water level fluctuation pattern in the Oude Waal. Due to the dry summer of 1976, vast areas of the Oude Waal became desiccated and numerous plants and animals died. Large numbers of Molluscs, particularly Bivalves such as *Unio pictorum* (L.), *Anodonta anatina* (L.) and *A. cygnaea* (L.), died in this period. At the rising of the water level in the period of January and February 1977, the shells of these animals released Ca^{2+}. But easily soluble elements like Mg^{2+} and SO_4^{2-} are also found in high concentrations, particularly in the shallower parts of the Oude Waal. Fig. 10 shows that Ca^{2+}, Mg^{2+} and SO_4^{2-}, and to a lesser extent also Cl^{-} and Na^{+}, were present in higher concentrations in the shallower parts than in the deeper parts of the Oude Waal, implicating that these elements are released from the bottom by rain water. Fig. 11 shows that the percolating water also influences the chemical composition of the water in the Oude Waal, e.g. the NO_3^{-}- and the tot. N-concentrations, while PO_4^{3-}-concentrations before the flooding are also much higher in the deeper parts than in the shallower parts (in this part of the country the groundwater shows rather high NO_3^{-}-concentrations).

The influence of flooding by water from the river Waal is particularly evident, since this water causes a dilution of most of the dissolved elements. The influence of rainfall on the chemical composition of the water in the Oude Waal can be seen in the higher concentrations of most ions in the shallower parts C_1 and C as compared to the deeper parts. The effect of percolation is seen in the rise in NO_3^{-}- and tot. N-concentrations in the deeper pond F.

4.3. PHYSICO-CHEMICAL CHARACTERISTICS OF THE DEEP POND F

From May 1977 to April 1978 pond F was sampled weekly. Samples were taken both in the open water area (F_1) and in the nymphaeid-dominated area (F_2). In addition, measurements of pH, temperature and oxygen content were undertaken. Table 3 summarizes the most important data (Roijackers, in press). In fig. 12 the concentrations of the P- and N-compounds have been plotted against time for both sampling localities; fig. 13 represents the thermal variation of both sampling localities and

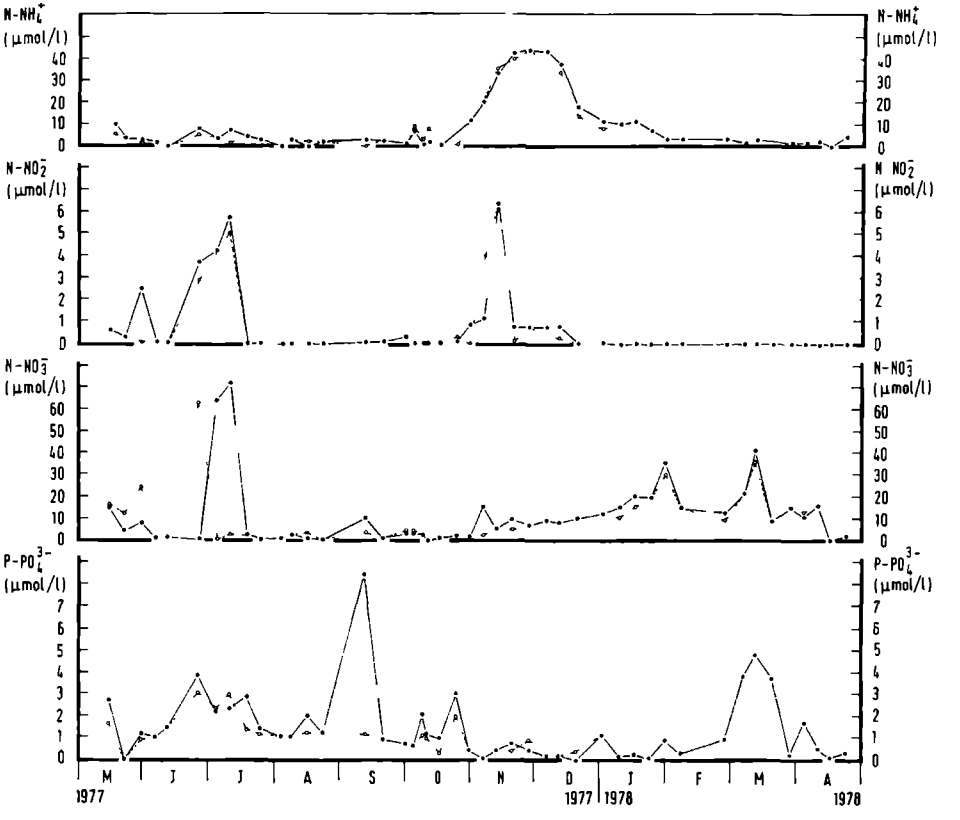


Fig. 12. The concentrations of N- and P-compounds in the water samples of sampling locality F_1 (open water area; solid line) and sampling locality F_2 (nymphaeid-dominated area; broken line) in pond F of the Oude Waal. Period: May 1977 to April 1978.

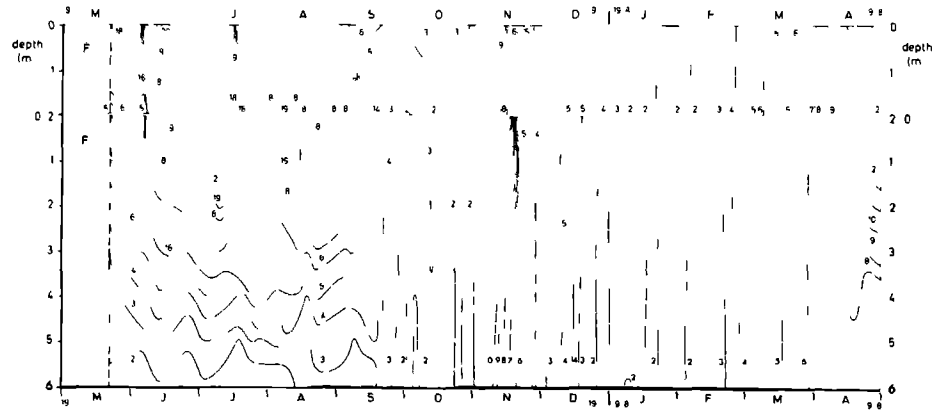


Fig. 13. Depth-time diagrams of isotherms (^{o}C) in pond F of the Oude Waal; Period: May 1977 to April 1978.
F_1 = open water area; F_2 = nymphaeid-dominated area.

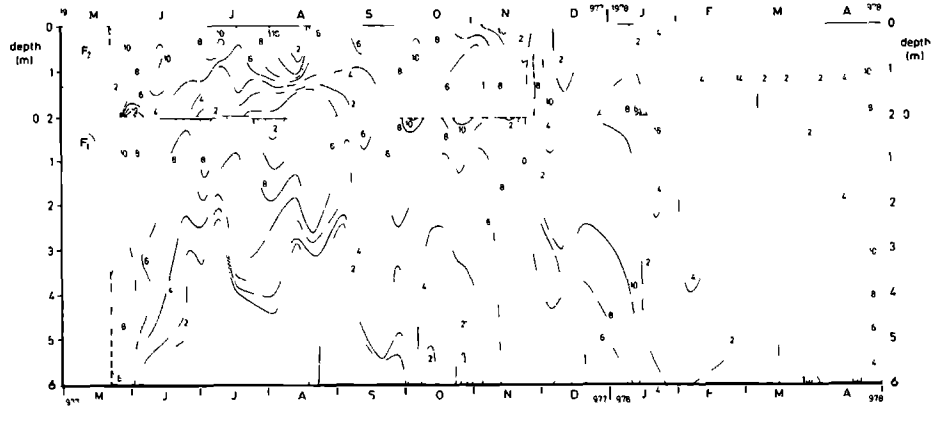


Fig. 14. Depth-time diagrams of isopleths of dissolved oxygen (mg/l) in pond F of the Oude Waal; Period: May 1977 to April 1978.
F_1 = open water area; F_2 = nymphaeid-dominated area.

Table 3. Principal physical and chemical characteristics of pond F of the Oude Waal (chemical compounds: mean concentrations plus standard deviation in µmol/l). F_1: open water part of the pond; F_2: nymphaeid-dominated part of the pond; period: 9 May 1977 to 24 April 1978.

	F_1	F_2
max. depth (m)	6.00	1.50
area (m^2)	13000	8000
K^+	142 ± 27	144 ± 35
Na^+	1490 ± 120	1471 ± 100
Ca^{2+}	2050 ± 360	1990 ± 370
Cl^-	1750 ± 440	1730 ± 450
SO_4^{2-}	570 ± 90	560 ± 80
PO_4^{3-}	0.5 ± 0.7	0.5 ± 0.6
Fe^{2+}	1.8 ± 2.1	2.4 ± 3.0
Mn^{2+}	3.0 ± 3.0	3.1 ± 3.2
Mg^{2+}	650 ± 70	620 ± 70
NH_4^+	6.2 ± 11.3	7.5 ± 20.2
NO_3^-	1.4 ± 2.0	1.2 ± 1.8
NO_2^-	0.2 ± 0.4	0.1 ± 0.4
HCO_3^-	4030 ± 790	4020 ± 810
pH min.	7.2	7.4
pH max.	8.3	8.4

fig. 14 represents the isopleths of dissolved oxygen. A bathymetric map of the pond is given in fig. 3.

It is evident from fig. 4 and table 3 that the main difference between the two parts of the pond is their depth, which causes a difference in macrophyte vegetation. The water chemistry can vary considerably from one year to another (compare table 3 with table 2; one must however keep in mind that the mean values of table 2 are based upon only 5 data from a limited period of time, while those of table 3 are based upon 44 data collected over a whole year!).

The differences in ionic composition of both sampling localities are negligible if the mean annual values are considered(table 3). In the nymphaeid-dominated area the pH is slightly higher than in the open water

area, indicating a higher primary production level in that locality. Pond F can be characterized as a highly eutrophic, hard-water surface water, the ratio of monovalent to divalent cations is 0.4, indicating favourable conditions for diatoms, as was already reported by Pearsall (1921, 1932).

As can be seen from figs. 3a and b and fig. 12 the Oude Waal was flooded only once in the period from May 1977 to April 1978, and the influence of this event cannot be traced in the concentrations of the dissolved nutrients. The changes in nutrient concentrations with time at F_1 and F_2 are almost always identical too. Only once was the $P\text{-}PO_4^{3-}$-content of the water at F_1 much higher than at F_2 (beginning of September 1977); this event coincided with the turnover of the water masses due to the decrease in temperature. Hence these high $P\text{-}PO_4^{3-}$-inputs most probably originate from the bottom layers of F_1.

Pond F is somewhat sheltered, which results in a thermal stratification which is stable for a long time (June to September) in the deeper parts of the pond (F_1). But in the shallower parts (F_2) thermal stratification also occurs, although this stratification can easily be disturbed by turbulence (fig. 13). The thermal stratification causes a stratification of dissolved oxygen (fig. 14). Hence this is another difference between the two sampling localities in pond F - stratification in summer - which will influence the phytoplankton comparisons.

4.4. PHYSICO-CHEMICAL CHARACTERISTICS OF THE SHALLOW POND D

From October 1978 to November 1979 pond D was sampled weekly. Samples were taken both in the open water area (D_1) and in the nymphaeid-dominated area (D_2). Measurements of pH, alkalinity, temperature, oxygen and irradiance were also carried out. In the field the degree of coverage by floating leaves of the nymphaeids was estimated. Table 4 summarizes the most important data (Roijackers, 1984b, in press). In fig. 15 the most important dissolved N-compounds have been plotted against time for both sampling localities. In fig. 16 the same has been done for the dissolved P-compounds; Fig. 17 represents the silica content of the water at D_1 and D_2. Fig. 18 illustrates the spectral absorption of the irradiance at several depths for the two sampling localities and fig. 19 shows the PhAR-irradiance at 15 cm below the water surface as well as the percentage

Table 4. Some chemical and physical characteristics of pond D of the Oude Waal, based on data from the sampling period 2 October 1978 to 22 October 1979. D_1: open water area; D_2: nymphaeid-dominated area. The concentrations of dissolved chemical compounds are given in µmol/l (mean plus standard deviations). The left-hand part of the table concerns mean values based upon the total investigation period, whereas the right-hand part of the table concerns mean values based upon the vegetative period (April 1979 to October 1979).

	D_1	D_2	D_1	D_2
max. depth (m)	1.80	1.50		
area (m^2)	9500	8000		
K^+	160 ± 52	157 ± 49	159 ± 53	151 ± 56
Na^+	1440 ± 250	1430 ± 260	1430 ± 140	1450 ± 140
Ca^{2+}	1210 ± 330	1180 ± 500	840 ± 210	790 ± 270
Cl^-	2140 ± 330	2120 ± 370	2410 ± 350	2515 ± 360
SO_4^{2-}	520 ± 210	510 ± 85	490 ± 120	460 ± 110
PO_4^{3-}	1.2 ± 1.5	1.1 ± 1.3	0.9 ± 1.3	0.6 ± 0.6
Fe^{2+}	0.5 ± 0.5	0.4 ± 0.3	0.3 ± 0.5	0.3 ± 0.3
Mn^{2+}	1.7 ± 1.5	1.6 ± 1.5	1.6 ± 1.9	0.9 ± 0.8
Mg^{2+}	580 ± 80	580 ± 90	580 ± 130	570 ± 100
NH_4^+	17.3 ± 17.8	17.2 ± 17.8	2.4 ± 5.6	3.7 ± 7.2
NO_3^-	14.8 ± 35.1	13.4 ± 33.9	1.5 ± 2.3	2.0 ± 4.1
NO_2^-	0.8 ± 0.9	0.8 ± 0.9	0.2 ± 0.3	2.0 ± 4.1
SiO_3^{2-}	47.6 ± 32.8	47.7 ± 33.2	49.7 ± 34.9	44.9 ± 31.7
tot. P	1.5 ± 1.2	1.5 ± 1.1	1.3 ± 0.9	1.4 ± 0.9
tot. N	54.3 ± 25.0	57.2 ± 28.6	40.4 ± 13.7	42.1 ± 17.2
pH min.	7.1	7.1		
pH max.	7.9	7.9		

of the surface covered by floating leaves of the nymphaeids at D_2; the water temperature as a function of time at D_1 (in this case exactly the same as at D_2) is presented in fig. 20. A bathymetric map of pond D is given in fig. 3.

The differences between D_1 and D_2 with respect to depth and chemical composition of the water are minimal (fig. 3; table 4). As in the case of pond F these mean values are not directly comparable to those mentioned in table 2. The pH of both sampling localities in pond D is slightly

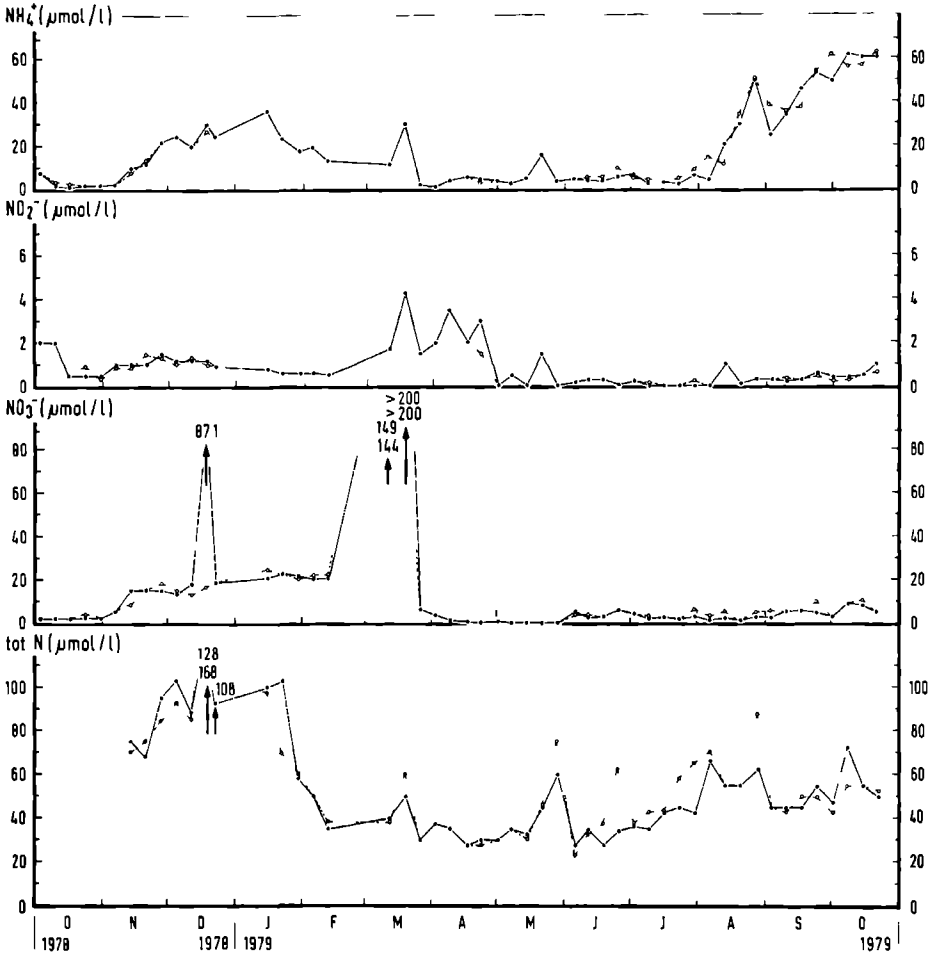


Fig. 15. The concentrations of N-compounds in the water samples of sampling locality D_1 (open water area; solid line) and sampling locality D_2 (nymphaeid-dominated area; broken line) in pond D of the Oude Waal. Period: October 1978 to November 1979.

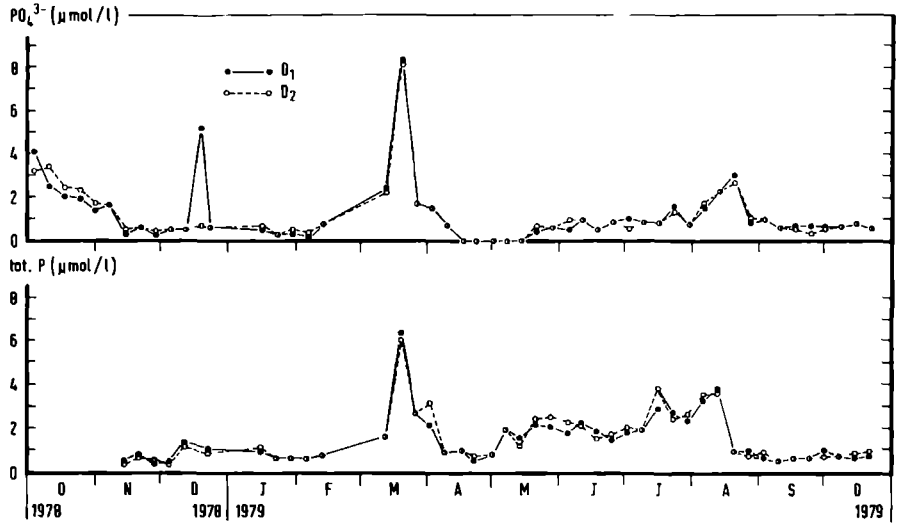


Fig. 16. The concentrations of P-compounds in the water samples of sampling locality D_1 (open water area; solid line) and sampling locality D_2 (nymphaeid-dominated area; broken line) in pond D of the Oude Waal. Period: October 1978 to November 1979

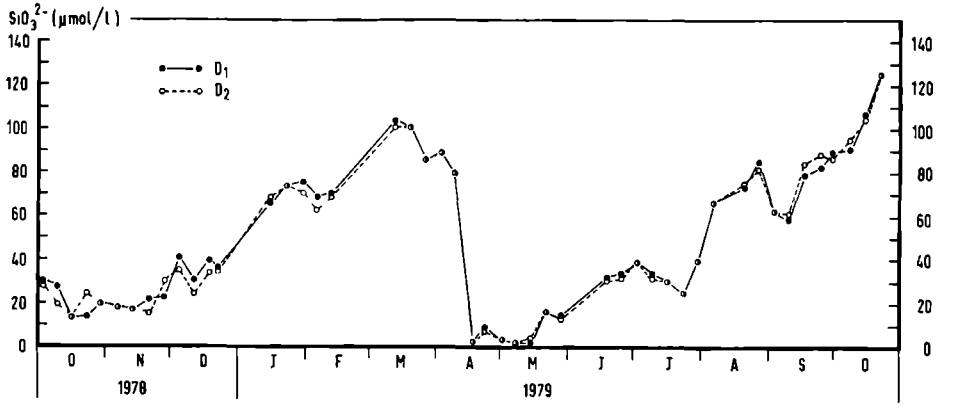


Fig. 17. The silica content of the water samples of sampling locality D_1 (open water area; solid line) and sampling locality D_2 (nymphaeid-dominated area; broken line) in pond D of the Oude Waal. Period: October 1978 to November 1979.

lower than that of the two sampling localities in pond F, indicating the higher microbial activity in the shallower pond D. Pond D is also a highly eutrophic, hard-water surface water; the ratio of monovalent to divalent cations is 0.6; somewhat higher than in pond F.

In table 4 the mean values of the ion concentrations are also given for the period in which the macrophytes are dominant. Marked differences occur in the Ca^{2+}-, NH_4^+- and NO_3^--concentrations, all of which are lower than the mean values found during the entire period of investigation. The NH_4^+- and NO_3^--concentrations are higher in the period after the vegetation period, partly as a result of the increased mineralization process and partly as a result of the absence of macrophytes which extract the oxidized N-compounds from the water for nutrition. The lower Ca^{2+}-concentrations during the vegetation period are the result of carbon assimilation by the macrophytes, which eventually leads to the precipitation of $CaCO_3$ (Hutchinson, 1967). The ratio of monovalent to divalent cations was the same for D_1 and D_2 if the entire period of investigation is considered. During the vegetation period the M/D-ratio was somewhat higher and differences are found between D_1 (0.82) and D_2 (0.87). Thus the M/D-ratio indicates more favourable (chemical) circumstances for the development of diatoms at D_2 during the vegetation period, when compared to D_1 during the same period. In comparing the N-, P-, and silica curves (fig. 15, 16 and 17) for both sampling localities no marked differences could be detected either; except for an unexplained high NO_3^-- and PO_4^{3-}-peak in December 1978 at D_1.

The flooding of the Oude Waal with water from the river Waal occurred in March 1979 and its influence can be traced in the large quantities of NO_3^- at that time.

The silica cycle as illustrated in fig. 17 is comparable to those reviewed by Hutchinson (1967) and Wetzel (1975). The silica content of the water in pond D is closely related to the presence of diatoms as will be shown in chapter 6 (see also Roijackers, 1984b).

The spectral composition of the irradiance at different depths at D_1 and D_2 (fig. 18) reflects the situation at only one particular day in September 1979, when the sky was cloudless. Measurements at D_2 were done at a place where the cover of floating leaves was 100%. Although these curves are based upon only one measurement it can be assumed that during

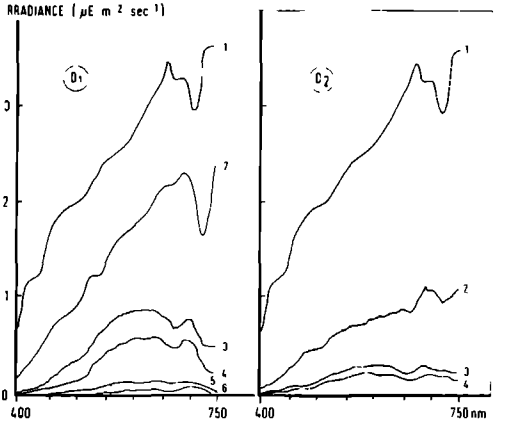


Fig. 18. The spectral composition of the irradiance at various depths at sampling localities D_1 (open water area) and D_2 (nymphaeid-dominated area) in pond D of the Oude Waal.
1 = incident irradiance; 2 = 10 cm depth; 3 = 25 cm; 4 = 50 cm; 5 = 100 cm; 6 = 150 cm.

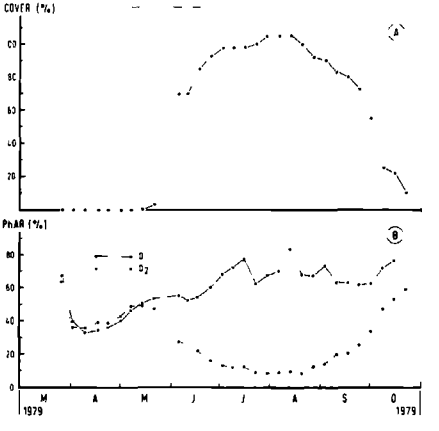


Fig. 19. A. The percentage of the surface covered by floating leaves of the nymphaeids at sampling locality D_2 (nymphaeid-dominated area) in pond D of the Oude Waal.
B. The irradiance level at a depth of 15 cm under the water surface at the sampling localities D_1 (open water area) and D_2 (nymphaeid-dominated area) in pond D of the Oude Waal.
Period: May to November 1979.

the period of maximum cover of the floating leaves of the nymphaeids at D_2 the illustrated irradiance climate exists permanently. Since the water column was supposed to be completely mixed vertically (chapter 3), and samples have therefore been taken at one fixed depth considered to be representative for the total water column, the influence of the differences in the spectral composition of the irradiance at different depths or localities has not been studied.

Fig. 19 illustrates the influence of the cover of floating nymphaeid leaves upon the total irradiance level at D_2 during the vegetation period. These curves show that the floating leaves of the nymphaeids account for up to 70% of the attenuation of the incident irradiance at a cover of 100%. These percentages of course depend on the absolute irradiance level and these high percentages (up to 75%) were found when the incident irradiance level was low; at high incident irradiance levels the attenuation by floating leaves was 30 to 50 percent.

Water temperatures at D_1 were the same as those at D_2. All measurements were done around 11.00 a.m., so variations during the day were not recorded (fig. 20).

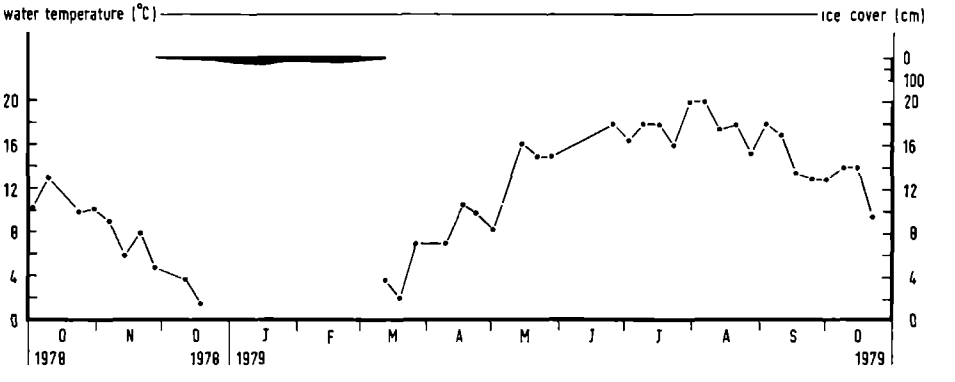


Fig. 20. The water temperature as a function of time at sampling locality D_1 (open water area) in pond D of the Oude Waal. Period: October 1978 to November 1979.

5. Previous and preliminary phytoplankton records from the Oude Waal

5.1 PREVIOUS PHYTOPLANKTON RECORDS

Previous phytoplankton records from the Oude Waal have been collected by Schroevers (1972), but the complete list of species encountered in his investigations has never been published. The list of species - kindly put at my disposal by Mr. P.J. Schroevers - has now been revised and taxonomical alterations have been made (table 5).

Schroevers' list of species is based upon identifications of preserved material (formaldehyde). It is surprising that common taxa such as *Cryptomonas* spp., some smaller loricate Chrysophytes, common Chlorococcales such as *Dictyosphaerium, Golenkinia, Micractinium* and some others are not found in the list. Neither have Euglenophytes been encountered. This is partly due to the method of fixation used and the method of sampling and subsampling. However, in comparing this list of species with that resulting from my own investigations (see next section, table 6 and appendices Ia+b) there are remarkable similarities. The list of species presented in table 6 is based upon lugol/formaldehyde-preserved samples, identified under an inverted microscope, which has less powerful lenses, due to that specific method used. This results in rough identifications as reflected by the considerable number of taxa only represented by their generic names. Furthermore some 'species' appear to represent form and size classes, rather than reliable species, for instance *Cryptomonas erosa* and *C. ovata*. It is obvious then, that also this method has its restrictions as far as the possibilities for identifying phytoplankton species are concerned.

Most species in Schroevers' list have been found in sampling locality C, where three samples were taken. Although these samples have been taken in open water localities within C, one must keep in mind that at the moment of sampling (June 1971) there was a rich macrophyte vegetation; this vegetation was highly diverse in C, so several quite different macrophyte stands were present, each with its own characteristic phytoplankton species composition, and all continuously exchanging phytoplankton material with the relatively small open water areas, thus also contributing to a highly diverse phytoplankton sample.

Table 5. Phytoplankton taxa found in samples from the Oude Waal as reported by Schroevers (1972) Taxa which here bear a different name from that used in Schroevers' original list of species have been indicated by an asterisk. These differences in names have been the result from taxonomical revisions.

	C	D_1	D_2	F
CYANOBACTERIA				
Chroococcus minutus (Kütz.) Näg.	+			
cf. Chroococcus spp.	+			
Dactylococcopsis raphidioides Hansg.	+			
Anabaena cf. utermöhlii Geitl.	+			
Anabaena spp.	+			
Oscillatoria tenuis Ag.	+			
Oscillatoria spp.	+	+		
Lyngbya limnetica Lemm.	+			
Lyngbya subtilis	+			
XANTHOPHYTA				
* Goniochloris fallax Fott	+			
* Goniochloris mutica (A. Br.) Fott	+	+		+
* Gon.ochloris smithii (Bourr.) Fott	+			
BACILLARIOPHYTA				
* Aulacosira granulata (Ehr.) Sim.	+	+		
Melosira varians Ag.	+	+	+	
Cyclotella meneghiniana Kütz.	+	+		
Cyclotella/Stephanodiscus spp.	+	+	+	+
Diatoma vulgare Bory	+			
Fragilaria construens (Ehr.) Grun.	+	+		+
Fragilaria crotonensis Kitt.	+			+
Fragilaria spp.	+	+		
Synedra acus Kütz.	+	+		
Synedra pulchella (Ralfs) Kütz.	+			
Synedra ulna (Nitzsch) Ehr.	+			
Cocconeis placentula Ehr.			+	
Cocconeis spp.		+		
Achnanthes exigua Grun.	+	+	+	
Achnanthes spp.		+		
* Rhoicosphenia abbreviata (Ag.) Lange B.	+	+		
Anomoeoneis sphaerophora (Kütz.) Pfitzer		+		
Navicula cryptocephala Kütz.	+	+	+	
Navicula cuspidata Kütz.	+			
Navicula dicephala (Ehr.) W. Smith	+			
Navicula gracilis Ehr.	+			
Navicula hungarica Grun.	+	+		+
Navicula radiosa Kütz.	+	+		
Navicula rhynchocephala Kütz.	+			
Navicula spp.	+	+		
Pinnularia gibba Ehr.		+		
Pinnularia spp.		+		
Neidium iridis (Ehr.) Cleve	+			
cf. Neidium spp.		+		
Caloneis silicula (Ehr.) Cleve	+			
Gyrosigma acuminatum (Kütz.) Rabenh.	+	+		
Gyrosigma attenuatum (Kütz.) Rabenh.	+			
Gyrosigma spp.		+		
Amphora ovalis Kütz.	+	+		
Cymbella ehrenbergii Kütz.	+			
Cymbella spp.	+	+	+	+
Gomphonema acuminatum Ehr.	+			
Gomphonema constric um Ehr.	+			
Gomphonema spp.	+			
Epithemia spp.	+			
Nitzschia filiformis (W. Smit.) Hust.	+			
Nitzschia linearis W. Smit.		+		
Nitzschia sigmoidea (Ehr.) W. Smith	+			
Nitzschia spp.	+	+	+	+
Cymatopleura solea (Bréb.) W. Smith	+			
Surirella robusta Ehr.	+			
CHLOROPHYTA				
Chlamydomonas spp.	+	+		+
Pharotus lenticularis (Ehr.) Stein	+			
Pandorina morum (O.F. Müller) Bory	+	+		
Eudorina elegan Ehr.	+			
* Sphaerocystis schroeteri Chod.	+		+	+
Chlorella vulgaris (Beijerinck) Emmr.	+			
Pediastrum boryanum (Turp.) Menegh.	+			
Pediastrum duplex Meyen	+			+
* Pediastrum duplex var. gracillimum W. et G.S. West	+			
Pediastrum tetras (Ehr.) Ralf.	+			
Oocystis lacustris Chod.	+			
Oocystis solitaria Wittr. in Wittr. et Nordst.	+		+	
Siderocelis ornata (Fott) Fott	+			
Siderocelis spp.	+			
Chlorella spp.	+			
* Monoraphidium convolutum (Corda) Kom.-Legn.	+			
* Monoraphidium griffithii (Berk.) Kom.-Legn.	+			
* Monoraphidium irregulare (G.M. Smith) Kom.-Legn.	+			
Elakatothrix spp.	+			+
Ankistrodesmus falcatus (Corda) Ralfs	+	+		
Ankistrodesmus/Monoraphidium spp.		+		
Tetraedron caudatum (Corda) Hansg.	+			+
Tetraedron minimum (A. Br.) Hansg.				
Coelastrum microporum Näg. in A. Br.	+		+	
Crucigenia quadrata Morr.	+	+		
Crucigenia tetrapedia (Kirchn.) W. et G.S. West	+			
Scenedesmus grunowii W. et G.S. West	+	+	+	+
Scenedesmus lefevrii Defl.	+	+		+
* Scenedesmus obtusus Meyen	+			
Scenedesmus quadricauda (Turp.) Bréb. sensu Chod.	+			
Scenedesmus spinosus Chod.	+			
Scenedesmus tenuispina Chod.	+			
Scenedesmus spp.	+	+		
Closterium venus Kütz. ex Ralfs	+			
Closterium spp.	+			
Cosmarium spp.	+			
Staurastrum gracile Ralfs	+			
Staurastrum paradoxum Meyen				+
Staurastrum tetracerum Ralfs	+	+		
REST-GROUP				
green spherical algae	+	+		+
green filamentous algae	+			
Total number of taxa	92	44	7	18

5.2. PRELIMINARY PHYTOPLANKTON STUDIES: CORRELATION WITH WATER LEVEL FLUCTUATIONS

In the period from January to May 1977 monthly samples were taken from C_1, C, D, E and F (fig. 1b). The phytoplankton species recorded during these investigations have been listed in table 6. Table 6 clearly shows that the differences between the sampling localities are not as pronounced as Schroevers' list suggests. This is partly due to the fact that all samples were taken in the period when the macrophytes were not yet developed. The only differences in species composition are a result of time and reveal the seasonal occurrence of species such as *Fragilaria capucina*, *F. crotonensis*, *Melosira varians*, *Gomphonema constrictum*, etc..

Since during the period of investigation the river Waal flooded the Oude Waal, the species composition of the phytoplankton at the different sampling localities could illustrate the influence of water level fluctuations upon the similarity in species composition of the phytoplankton at the different sampling localities. For this reason the similarity between the four localities C, D, E and F was computed on the basis of the absence and/or presence of the phytoplankton species according to the Sørensen similarity index (Sørensen, 1948). Fig. 21 shows this similarity index for the five sampling dates in relation to water level fluctuations in the Waal and the Oude Waal.

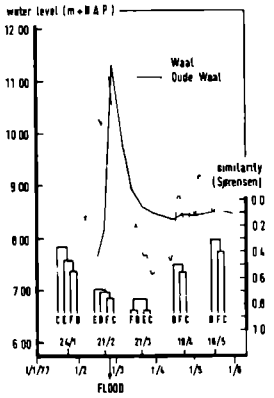


Fig. 21. The similarity (based upon phytoplankton species composition and the Sørensen similarity coefficient) between the sampling localities C, D, E and F in the the Oude Waal in relation to the water level fluctuations in the Oude Waal and the river Waal.
Period: January to May 1977.
Sampling locality E has not been sampled in April and May.

Table 6. Phytoplankton taxa found in samples from the Oude Waal during the investigations from January to May 1977.

CYANOPHYTA	C1	C	D(1)	E	F(1)
Anacystis spp	+	+		+	+
Merismopedia spp	+				
Oscillatoria spp	+	+			
CHRYSOPHYTA					
Chrysococcus spp	++++	++++	+++ +	++	++
Dinobryon spp	++	+	+	+	+
XANTHOPHYTA					
Tribonema spp	+	+			
BACILLARIOPHYTA					
Aulacosira granulata (Ehr) Sim	+	+	+		+
Melosira varians Ag	+	+	+ +	+ +	+ +
Cyclotella comta (Ehr) Kutz	+ +++	+++ +	+ ++	+ +	+ ++
Cyclotella meneghiriana Kutz	+ ++	+++++	+++++	+++	+++++
Meridion circulare Ag				+	+
Diatoma elongatum (Lyngb) Ag	+++++	+++	+ ++	++	+ +++
Diatoma vulgare Bory	++++	++++	++++	+++	++++
Fragilaria capucina Desm	+	+ ++	+ ++	+	++
Fragilaria construens (Ehr Grun	+++++	++++	+++++	++	++++
Fragilaria crotonensis Kitton	+	++	+		+ ++
Fragilaria vaucheriae Kutz	+		+	++	+
Asterionella formosa Hassall	+++	++++	+ +++	+ +	++++
Eunotia lunaris (Ehr) Grun	+ +	+	+	++	
Cocconeis placentula Ehr			+		+
Cocconeis scutellum Ehr	+++++	+++++	+++++	+++	+++++
Achnanthes affinis Grun	+++	+++	+		+
Achnanthes lanceolata (Bréb) Grun	+++++	+++++	++++	+++	+++++
Achnathes microcephala (Kutz) Grun	+		+	+	+++
Diploneis ovalis (Hilse) Cleve					+
Frustulia rhomboides (Ehr) De Toni				++	
Navicula anglica Ralfs	+ ++	+ ++	+ +	+	+
Navicula cryptocephala Kütz	+++++	+++++	+++++	+++	+++++
Navicula exigua (Greg) O F Müller	+	+ +	+ +++	+++	+ +++
Navicula gracilis Ehr			+		
Navicula lacusstris Greg		+	+	+	+
Navicula protracta (Grun) Cleve	++++	+++ +	+++	+++	+++++
Navicula radiosa Kütz	+++++	+++++	+++++	+++	+++++
Navicula rhynchocephala Kütz	+++++	+++++	+++	+++	+++++
Navicula rotaeara(Rabenh) Grun			+		
Gyrosigma attenuatum (Kutz) Rabenh	+	++ ++	+ +	+++	+ +
Cymbella microcephala Grun			+	+	+
Cymbella prostrata (Berk) Cleve		+			+
Cymbella turgida Greg) Cleve	+ +++	++ +	++ +	+++	+- ++
Gomphonema olivaceum (Lyngb) Kutz	+++ +	+++++	+ +++	+++	++++
Gomphonema acuminatum Ehr	+ +++	+++	+-++	+-	+ +
Goephonema constrictum Ehr	+ ++	++	++	+	+ -
Gomphonema parvulum (Kütz) Grun					+
Epithemia turgida Ehr) Kütz			+	-	-
Nitzschia acicularis W Smith	++++-	+ +++	+ +++	+	+ +
Nitzschia hungarica Grun	++ +	++	+	++	++
Nitzschia linearis W Smith	+++++	++++	++++	++	++++
Nitzschia palea (Kutz) W Smith	+++++	+ +++	++++	+	+ ++
CRYPTOPHYTA					
Cryptomonas erosa Ehr	+++	+++++	+++ +	+++	++ +
Cryptomonas ovata Ehr	++++	+++++	+++++	+++	+++++

PYRRHOPHYTA	C1	C	D(1)	E	F(
Peridiniopsis spp	+				
Peridinium spp	++	+++	++++	++	++
Ceratium hirundinella (O F Muller) Schrank	++	++	++ ++	+++	++ ++
EUGLENOPHYTA					
Euglena spp	+++	+++	+++++	+++	+++
Phacus pleuronectus (O F Muller) Duj		+			
Phacus spp	+++	+	+	+	++
Trachelomonas hispida (Perty) Stein			+		
Trachelomonas volvocina Ehr	++	+	+	+	+ + +
Trachelomonas spp	+++++	+++++	++++	++	+++ +
CHLOROPHYTA					
Chlamydomonas spp	++++	++++	+++ +	+++	++++
Chlorogonium elongatum (Dang) Jarg	++	+++	++	+	+ +
Gonium pectorale O F Müller		+	++		
Pandorina morum (O F Muller) Bory	++	++	++++	+	+ ++
Eudorina elegans Ehr	+++	++	+++	+	+
Tetraspora spp		+			
Treubaria triappendiculata Bernard				+	
Pediastrum boryanum (Turp) Menegh		+ +	+++++	+++	+ +
Pediastrum duplex Meyen	++	+	+ +		
Pediastrum spp					+
Dictyosphaerium pulchellum Wood		+	++		
Oocystis spp	+	+		+	+
Monoraphidium minutum (Näg) Kom Legn					+ +
Kirchneriella lunaris (Kirchn) Möb				+	
Kirchneriella spp		+			
Ankistrodesmus falcatus (Corda) Ralfs	+++	++	+++ +	++	+ +++
Ankistrodesmus gracilis (Reinsch) Korsh		+	+	++	+
Ankistrodesmus/Monoraphidium spp	+	++	+	+ +	+
Tetraedron minimum (A Br) Hansg			+		+
Tetraedron spp		+			
Coelastrum microporum Näg in A Br				+	+
Tetrastrum staurogeniaeforme (Schr) Lemm			++		+
Crucigenia fenestrata(Schmidle) Schmidle		+	+	+	
Crucigenia quadrata Morr	++	++++	++++	+++	++++
Crucigenia tetrapedia (Kirchn) W et G S West		+	+	+	
Scenedesmus acuminatus (Lagerh) Chod	+	+	+++	+	
Scenedesmus dimorphus (Turp) Kütz			+		
Scenedesmus granulatus W et G S West			+		
Scenedesmus hystrix Lagerh	+	+			
Scenedesmus quadricauda (Turp) Bréb sensu Chod	+++	++ +	+++++	++	++
Scenedesmus spp	++	++ +	+-	+++	++++
Ulothrix spp	+				
Oedogonium spp	+				
Zygnema spp			+		
Spirogyra spp	++				
Closterium acerosum Schr) Ehr ex Ralfs	++		+		+
Closterium lunula (Müll) Nitzsch ex Ralfs					+
Closterium moniliferum Bory Ehr ex Ralfs					+
Closterium praelongum Bréb			+		
Closterium spp			+		
Total number of taxa	63	67	73	62	70

It is apparent from fig. 21 that the water level in the Oude Waal was very low in the beginning of February (and also in January; both due to the very dry summer of 1976) and rose quickly due to percolating water and rainfall, which meant that the four sampling localities became more and more interconnected. At the same time an increase in phytoplankton similarity between the four sampling localities can be observed. On February 24th, all of the Oude Waal was flooded and well mixed. This is reflected by the extremely high similarity between the phytoplankton species composition at the four sampling localities, which at that moment were in open connection. After April 1977 the water in the Oude Waal fell to a 'normal' level and the four parts were from that moment on only interconnected by very shallow 'channels' (fig. 1b). This most probably put an end to the continuous exchange of phytoplankton inoculation material, enabling the four parts of the Oude Waal to develop their own phytoplankton communities, which is shown in fig. 21 as a steep decline in similarity as regards their species composition in April and May 1977.

It is obvious, then, that the species composition of phytoplankton is greatly influenced by water level fluctuations. It should be noted that from the moment the water in the Oude Waal reached its 'normal' level, exchange of phytoplankton species from one locality to the other by means of direct water movements becomes highly unlikely.

5.3. PRELIMINARY PHYTOPLANKTON STUDIES: CORRELATION WITH WATER DEPTH

From May 1977 to April 1978 pond F was sampled weekly at the localities F_1 and F_2. Apart from the physico-chemical investigations (see chapter 4) samples for phytoplankton studies were also taken. Sampling procedures and subsequent analyses were described in chapter 3.

Phytoplankton species are listed in appendices Ia and b. These appendices also include their frequency (frequency class 1 meaning: the taxon is present in 1-20% of the samples taken throughout the investigation period; 2: 21-40%; 3: 41-60%; 4: 61-80%; 5: 81-100%). A considerably condensed list of species is presented here in table 7a and b. These tables include only the most frequent taxa (frequency classes 5, 4 or 3). The following phytoplankton characteristics were determined: species composition, relative abundance of the species, chlorophyll-a content and ashfree dry weight. The chlorophyll-a content as a function of time

Table 7a. Taxa at sampling locality F_1 with a frequency class 5 (first column left), 4 (second column left) or 3 (right column). 5 = present in 81-100% of the samples; 4 = present in 61-80% of the samples; 3 = present in 41-60% of the samples.

Cyclotella meneghiniana	Dinobryon divergens
Asterionella formosa	Mallomonas caudata
	Mallomonas akrokomos
	Mallomonas spp.
	Paraphysomonas spp.
Chrysococcus spp.	Aulacosira granulata
Stephanodiscus hantzschii	Fragilaria crotonensis
Diatoma elongatum	Fragilaria vaucheriae
Synedra ulna	Synedra acus
Cocconeis pediculus	Cocconeis placentula
Navicula cryptocephala	Gomphoneis olivaceum
Cryptomonas erosa	Nitzschia palea
Cryptomonas ovata	Gymnodinium spp.
Cryptomonas spp.	Trachelomonas hispida
Peridinium spp.	Pandorina morum
Trachelomonas volvocina	Oocystis spp.
Chlamydomonas spp.	Monoraphidium minutum
Ankistrodesmus falcatus	Ankistrodesmus spiralis
Scenedesmus quadricauda	Tetrastrum staurogeniaeforme
	Scenedesmus granulatus

Table 7b. Taxa at sampling locality F_2 with a frequency class 5 (first column left), 4 (second column left) or 3 (right column). 5 = present in 81-100% of the samples; 4 = present in 61-80% of the samples; 3 = present in 41-60% of the samples.

Cyclotella meneghiniana	Mallomonas caudata
	Mallomonas spp.
	Synura spp.
	Chromophysomonas spp.
Chrysococcus spp.	Paraphysomonas spp.
Stephanodiscus hantzschii	Aulacosira granulata
Fragilaria vaucheriae	Melosira varians
Synedra acus	Diatoma elongatum
Asterionella formosa	Navicula cryptocephala
Cocconeis pediculum	Navicula radiosa
Cocconeis placentula	Gyrosigma acuminatum
Achnanthes hauckiana	Amphora ovalis
Cryptomonas erosa	Gomphoneis olivaceum
Cryptomonas ovata	Nitzschia palea
Cryptomonas spp.	Gymnodinium spp.
Chlamydomonas spp.	Peridinium spp.
Scenedesmus quadricauda	Trachelomonas hispida
	Trachelomonas volvocina
	Lagerheimia genevensis
	Oocystis spp.
	Ankistrodesmus falcatus
	Ankistrodesmus spiralis
	Tetrastrum staurogeniaeforme
	Scenedesmus granulatus

is shown in fig. 22, the ashfree dry weight is shown in fig. 23.

Tables 7a and b make it possible to define the basic combination of phytoplankton taxa occurring at pond F. This combination consists of those taxa present in the pond throughout the year (frequency classes 5 and 4). The following combination is characteristic for pond F:

Chrysococcus spp.
Cyclotella meneghiniana
Stephanodiscus hantzschii
(Diatoma elongatum)
(Fragilaria vaucheriae)
(Synedra acus)
Synedra ulna
Asterionella formosa
(Cocconeis pediculus)
Cocconeis placentula
(Navicula cryptocephala)
Cryptomonas erosa
Cryptomonas ovata
Cryptomonas spp.
(Peridinium spp.)
(Trachelomonas volvocina)
Chlamydomonas spp.
(Ankistrodesmus falcatus)
Scenedesmus quadricauda

Those taxa in this list having a frequency class 3 in either F_1 or F_2 have been put between brackets. The list could be supplemented by the species

Achnanthes hauckiana

which has a frequency class 4 at F_2 and a frequency class 2 at F_1. As will be shown in chapter 6, this combination of species is also characteristic for pond D and could be considered characteristic for the entire Oude Waal system.

In order to trace differences in the frequency of occurrence of the taxa in relation to the presence of absence of the above-ground nymphaeid vegetation, appendices Ia and b also give the frequencies of the taxa during the period of maximum development of the nymphaeids (May-September

1977)and during the absence of the above-ground nymphaeid biomass (October 1977 - April 1978). Where the frequency classes in those two periods differ more than 2 units, the differences are supposed to be significant. And where the results for sampling locality F_1 are the same as for sampling locality F_2 these differences can be attributed to the seasonal development of the phytoplankton. But where the differences are not the same for F_1 and F_2, a connection with the above-ground biomass of the nymphaeids is highly probable. In this way the taxa could be grouped into four categories:

a. taxa which are present particularly during the period of nymphaeid development, but whose presence is not influenced by the nymphaeids:

Anabaena flos-aquae
Tribonema spp.
Cocconeis placentula
Cymbella prostrata
Gomphonema constrictum
Nitzschia dissipata
Nitzschia linearis
Nitzschia palea

b. taxa which are present particularly during the period in which the nymphaeids are in dormancy, but whose absence during the period of nymphaeid development is not influenced by the nymphaeids:

Chrysococcus spp.
Kephyrion haemisphaericum
Stenokalyx monilifera
Pseudokephyrion entzii
Mallomonas akrokomos
Mallomonas/Mallomonopsis spp.
Synura petersenii
Chromophysomonas spp.
Bicocoeca planktonica
Stephanodiscus hantzschii
Fragilaria vaucheriae
Asterionella formosa
Eunotia lunaris
Achnanthes hauckiana

Navicula cincta
Navicula hungarica
Gomphonema parvulum
Cryptomonas erosa
Cryptomonas spp.
Gymnodinium spp.
Peridinium spp.
Trachelomonas hispida
Trachelomonas volvocina
Chlamydomonas spp.
Lagerheimia genevensis
Oocystis spp.
Monoraphidium minutum
Ankistrodesmus spiralis
Tetrastrum staurogeniaeforme
Crucigenia tetrapedia
Scenedesmus granulatus

c. taxa which are present during the period of nymphaeid development and particularly in the nymphaeid-dominated part of the pond:

Fragilaria bidens

d. taxa which are present during the period of nymphaeid development and particularly present in the open water area of the pond:

Synedra acus
Synedra tabulata var. *fasciculata*

These lists clearly show that the phytoplankton species composition in pond F is not strongly determined by the presence or absence of the nymphaeids. Table 8 shows the succession in dominant phytoplankton taxa for the open water area of the pond (F_1); the situation is essentially the same for sampling locality F_2 (nymphaeid-dominated part of the pond). Table 8 shows that some taxa are dominant for a longer period of time, while other taxa dominate for a short period only. Particularly during the colder part of the year some taxa remain dominant for several months. In the case of *Chrysococcus* spp. several species of this genus could be involved. It is striking that the centric diatom *Cyclotella meneghiniana* remains dominant for over 6 months, while the chrysophyte genus *Chrysococcus* remains dominant for as much as 8 months! This indicates a rather stable phytoplankton community, which, apart from the persistant dominants,

Table 8. Succession in dominant phytoplankton taxa at sampling locality F_1 (open water area) in pond F of the Oude Waal. The information is based upon abundance estimates. The names have been abbreviated.

M	J	J	A	S	O	N	D	J	F	M	A
Mall akro											
Chla spp											
Aky anco											
Quad clos											
	Anab flos										
	Dino dive										
	Cycl mene	Cycl mene	Cycl mene	Cycl mene	Cycl mene	Cycl mene					Cycl mene
	Step hant							Step hant	Step hant	Step hant	
		Aula gran									
		Mall caud									
			Chry spp	Chry spp	Chry spp	Chry spp	Chry spp	Chry spp	Chry spp	Chry spp	Chry spp
			Pter angu	Pter angu							
				Trac oblo							
				Trac volv							
				Peri spp	Peri spp						Peri spp
								Cryp spp	Cryp spp	Cryp spp	
								Anki spir	Anki spir	Anki spir	
										Synu pete	Synu pete
											Oocy spp
											Aste form

shows great diversity in its species composition.

The phytoplankton biomass is rather low (maximum values for chlorophyll-a content: 53 µg/l and for the ashfree dry weight: 5.8 mg/l). There are biomass peaks in October 1977 (*Cyclotella meneghiniana* and *Chrysococcus* spp.) and in March/April 1978 (*Chrysococcus* spp., *Synura petersenii*, *Stephanodiscus hantzschii* and *Cyclotella meneghiniana*). The phytoplankton biomass fluctuation pattern in pond F is typical for a shallow productive lake (Reynolds, 1984).

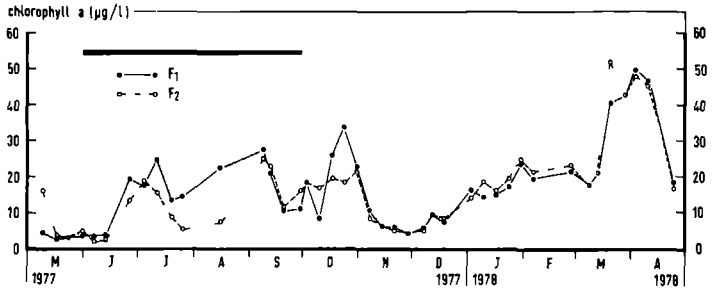


Fig. 22. Chlorophyll-a content of the phytoplankton in pond F of the Oude Waal. F_1 = open water area; F_2 = nymphaeid-dominated area. The period of maximum development of the floating leaves of the nymphaeids is indicated.

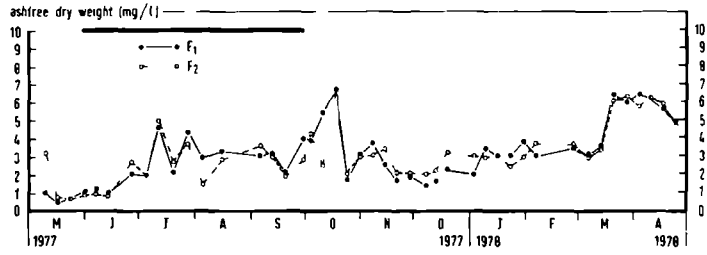


Fig. 23. Ash-free dry weight of the seston in pond F of the Oude Waal. F_1 = open water area; F_2 = nymphaeid-dominated area. The period of maximum development of the floating leaves of the nymphaeids is indicated.

5.4. DISCUSSION

It is clear that an investigation of the phytoplankton community structure in any surface water must be based upon a frequent sampling program. Theoretically a phytoplankton investigation carried out only once will reveal the most frequent taxa plus some taxa characterizing that specific moment of sampling. It is therefore surprising that the list of species given by Schroevers (1972) revealed no more than 10 percent of the frequent taxa (present for over 61% of the year) in pond F. Of the most frequent species, none was reported by Schroevers (these species are present during more than 81% of the year: *Cyclotella meneghiniana* and *Asterionella formosa*). Even if all the taxa in Schroevers' list, present at either C_1, D_1, D_2 or F_1, are taken into account, only 55% of the frequent taxa are recorded and only one of the two most frequent species (*Cyclotella meneghiniana*).

Preliminary investigations (January to May 1977) also included pond F. During these investigations 75% of the frequent taxa were recorded, including the two most frequent species. It is possible that since Schroevers' inventory of the phytoplankton of the Oude Waal a change has occurred in the Oude Waal which has caused a drastic and permanent change in the phytoplankton community structure. This could only have happened before 1977 as the lists of species from that year are entirely comparable

to later lists. Such a change has never been reported. It is also possible that the year 1971 (the actual year of Schroevers' visit to the Oude Waal) was an exceptional year as regards the environmental conditions. This again is not found in any of the reports.

It must, then, be concluded that the phytoplankton community structure is inadequately described by an investigation of the phytoplankton species composition during just one sampling trip. A better picture is given by a monthly sampling frequency. The preliminary phytoplankton investigations at pond F from May 1977 to April 1978 resulted in a good picture of the phytoplankton species composition and succession and of the phytoplankton biomass development. It is, however, questionable whether the differences in depth of both sampling localities F_1 (open water area: 6 m) and F_2 (nymphaeid-dominated area: 1.5 m) did not interfere with the possible effects of the nymphaeids upon the phytoplankton community structure.

In the actual study, therefore (which will be dealt with in the next chapters) the phytoplankton in pond D was studied, as in pond D both localities D_1 (open water area) and D_2 (nymphaeid-dominated area) have about the same maximum depth (1.8 m and 1.5 m respectively).

6. STRUCTURAL CHARACTERISTICS OF THE PHYTOPLANKTON COMMUNITIES IN POND D

6.1. SPECIES COMPOSITION

Phytoplankton communities consist of a wide variety of taxa. The phytoplankton communities show temporal variations both in species composition and in number of individuals, as a result of the fluctuations in the environment and the life cycles of the organisms themselves. Species composition is thus a basic structural characteristic of phytoplankton communities.

In chapter 3 section 3.1.3. some attention has been paid to the 'plankton paradox' as observed by Hutchinson (1961). It was also pointed out in that section that the methods used in my investigations are not adequate for the detection of the actual spatial phytoplankton distribution such as would be needed for a strengthening of the theory of the 'contemporaneous disequilibrium' (Richerson et al., 1970), which explains part of the plankton paradox. And although the sampling frequency was increased to as much as once a week, this was still not enough to detect the basic changes in the metabolism of the algae and the changes in the species composition of the communities which eventually result from these basic changes.

The identification of phytoplankton species is laborious and in many cases identifications at species level are impossible, as special time-consuming techniques have to be applied, such as culturing, in vivo dying, the use of special microscopes, etc. Despite my profound conviction that only a taxon correctly identified down to the species level will give clear information, I did not succeed in identifying all the taxa concerned. The above mentioned special techniques have been used only in those cases in which identification down to species level was technically possible and also necessary, because the taxa constituted an important structural element in the phytoplankton communities.

Within the phycological classification the arrangement of algae changes often on the basis of new insights resulting from taxonomical work. There is no universally accepted classification scheme, although the general outlines of the various schemes are the same (see for instance Round, 1981; Reynolds, 1984). In the last 10 to 20 years many revisions in the arrangement of algae have been proposed in order to account for newly discovered

taxa, and for new insights resulting from especially ultrastructural investigations and the culturing of algae (cf. for instance Bourrelly, 1968 and 1981; Fott, 1971 and Ettl, 1980; van den Hoek, 1978; Komarek & Fott, 1983). The classification scheme used here is based on that of Christensen (1962), but several deviations from it have been accepted.

The following sections deal with the Cyanobacteria, Xanthophyta, Cryptophyta, Pyrrhophyta, Euglenophyta and Chlorophyta (section 6.1.1.), the Chrysophyta and Prymnesiophyta (section 6.1.2.) and the Bacillariophyta (section 6.1.3.), thus subdividing the total phytoplankton list (given as appendices IIa and b for sampling localities D_1 (open water area) and D_2 (nymphaeid-dominated area) respectively) into three groups on the basis of their specific identification methods and relative importance in the phytoplankton communities. The discrepancies between the appendices and the specific species lists dealt with in sections 6.1.2. and 6.1.3. are the result of discrepancies in the methods used. The taxa mentioned in the appendices have been identified by means of light microscopy, using phase-contrast and drops of living non-preserved sample material, whereas the taxa mentioned in the tables of sections 6 1.2. and 6.1.3. have been identified with the help of the specific methods described in chapter 3, section 3.3.

6.1.1. Cyanobacteria, Xanthophyta, Cryptophyta, Pyrrhophyta, Euglenophyta and Chlorophyta

These taxa have not been identified with the help of specific identification methods and are listed in appendix IIa for the open water area of pond D (D_1) and in appendix IIb for the nymphaeid-dominated area of that pond (D_2). Taxa encountered in more than 10 percent of the samples from sampling localities D_1 and D_2 are listed in table 9 and table 10 respectively. A short comment on these lists from a taxonomical point of view will be given here.

Cyanobacteria

The number of taxa encountered in the samples is surprisingly low. This is partly due to the problem of distinguishing between bacteria and blue-green algae, a problem which has led to the creation of the combined group of the Cyanobacteria. As a result, some coccoid blue-greens of the genera *Aphanothece* and *Aphanocapsa* have not been identified as such; other genera,

Table 9. The presence of phytoplankton taxa (other than Chrysophyta, Prymnesiophyta and Bacillariophyta) in the samples taken from sampling locality D_1 (open water area) in pond D of the Oude Waal in the period October 1978 to November 1979.
Only those taxa have been included which were present in more than 10 % of the 48 samples. Frequency classes are given for a: the entire period, b: the vegetation period, c: beyond the vegetation period.

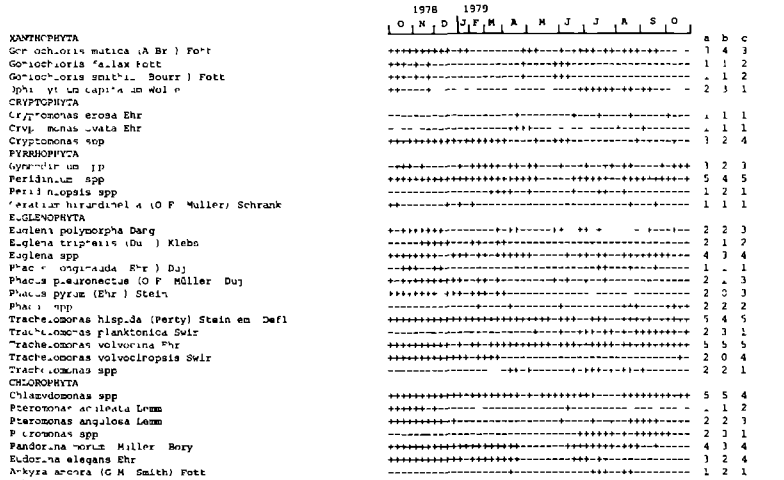
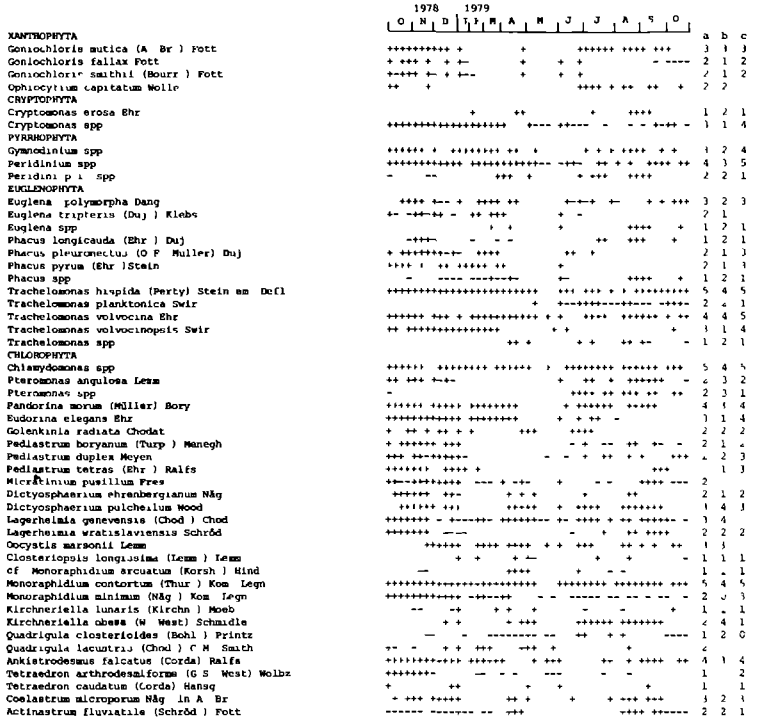


Table 10. The presence of phytoplankton taxa (other than Chrysophyta, Prymnesiophyta and Bacillariophyta) in the samples taken from sampling locality D_2 (nymphaeid-dominated area) in pond D of the Oude Waal in the period October 1978 to November 1979. Only those taxa have been included which were present in more than 10 % of the 48 samples. Frequency classes are given for a: the entire period, b: the vegetation period, c: beyond the vegetation period.



	a	b	c
XANTHOPHYTA			
Goniochloris mutica (A Br) Fott	3	3	3
Goniochloris fallax Fott	2	1	2
Goniochloris sculpta (Bourr) Fott	2	1	2
Ophiocytium capitatum Wolle	2	2	
CRYPTOPHYTA			
Cryptomonas erosa Ehr	1	2	1
Cryptomonas spp	3	1	4
PYRRHOPHYTA			
Gymnodinium spp	3	2	4
Peridinium spp	4	3	5
Peridinium spec spp	2	2	1
EUGLENOPHYTA			
Euglena polymorpha Dang	3	2	3
Euglena tripteris (Duj) Klebs	2	1	
Euglena spp	1	2	1
Phacus longicauda (Ehr) Duj	1	2	1
Phacus pleuronectes (O F Muller) Duj	2	1	3
Phacus pyrum (Ehr) Stein	2	1	3
Phacus spp	1	2	1
Trachelomonas hispida (Perty) Stein em Defl	5	4	5
Trachelomonas planktonica Swir	2	2	1
Trachelomonas volvocina Ehr	4	4	5
Trachelomonas volvocinopsis Swir	3	1	4
Trachelomonas spp	1	2	1
CHLOROPHYTA			
Chlamydomonas spp	5	4	5
Pteromonas angulosa Lemm	4	3	2
Pteromonas spp	2	3	1
Pandorina morum (Müller) Bory	4	4	4
Eudorina elegans Ehr	3	1	4
Golenkinia radiata Chodat	2	2	2
Pediastrum boryanum (Turp) Menegh	2	1	2
Pediastrum duplex Meyen	2	2	3
Pediastrum tetras (Ehr) Ralfs	1	2	3
Micractinium pusillum Fres	2		
Dictyosphaerium ehrenbergianum Näg	2	1	2
Dictyosphaerium pulchellum Wood	3	4	3
Lagerheimia genevensis (Chod) Chod	3	4	
Lagerheimia wratislaviensis Schröd	2	2	2
Oocystis marssonii Lemm	1	3	
Closteriopsis longissima (Lemm) Lemm	1	1	1
cf Monoraphidium arcuatum (Korsh) Hind	1	1	1
Monoraphidium contortum (Thur) Kom Legn	5	4	5
Monoraphidium minimum (Näg) Kom Legn	2	3	3
Kirchneriella lunaris (Kirchn) Moeb	1	1	1
Kirchneriella obesa (W West) Schmidle	4	4	1
Quadrigula closterioides (Bohl) Printz	2	2	0
Quadrigula lacustris (Chod) G M Smith	4		
Ankistrodesmus falcatus (Corda) Ralfs	4	4	4
Tetraedron arthrodesmiforme (G S West) Wolbz	1		2
Tetraedron caudatum (Corda) Hansg	1		1
Coelastrum microporum Näg in A Br	3	2	1
Actinastrum fluviatile (Schröd) Fott	2	2	1
Actinastrum hantzschii Lagerh	1		1
Westella botryoides (W West) De Wild	1		1
Tetrastrum glabrum (Roll) Ahlstr et Tiff	2		3
Tetrastrum punctatum (Schmidle) Ahlstr et Tiff	2	1	1
Tetrastrum staurogeniaeforme (Schröd) Lemm	3	1	4
Willea irregularis (Wille) Schmidle	2	2	1
Crucigenia fenestrata (Schmidle) Schmidle	1		
Crucigenia quadrata Morr	2	2	2
Crucigenia tetrapedia (Kirchn) W et G S West	3	3	4
Crucigeniella rectangularis (Näg) Kom	1	2	1
Scenedesmus acuminatus var acuminatus (Lagerh) Chod	1		2
Scenedesmus acuminatus var biror G M Smith	1		2
Scenedesmus bicaudatus Dedus	2	2	2
Scenedesmus denticulatus Lagerh	1	0	
Scenedesmus dimorphus (Turp) Kütz	3	3	1
Scenedesmus ecornis var ecornis (Ehr) Chod	1	0	2
Scenedesmus granulatus W et G S West	2	0	3
Scenedesmus longispina Chod	1	2	1
Scenedesmus quadricauda (Turp) Bréb sensu Chod	4	4	3
Scenedesmus sempervirens Chod	1		1
Scenedesmus spinosus Chod	2	0	2
Scenedesmus tenuispina Chod	2	2	2
Closterium pronum Bréb	2		3
Cosmarium spp	3	3	2
Staurastrum tetracerum Ralfs	2	2	2

such as *Microcystis, Gomphosphaeria, Coelosphaerium* and *Chroococcus* have not been encountered in the samples. The genus *Dactylococcopsis* is highly doubtful and I am almost convinced that the *Dactylococcopsis*-like taxa which I have seen were decaying *Monoraphidium*- or *Ankistrodesmus*-species (Chlorophyta).

Xanthophyta

Xanthophyta, and particularly the coccoid forms, are not as easy to identify as Ettl (1978) would have it. This is entirely due to the fact that in most ecological studies one is dealing with a wide diversity of taxa, comprising several phyla, of which the Xanthophyta constitute one and the Chlorophyta another. Several forms within the Xanthophyta resemble forms belonging to the Chlorophyta (particularly the Chlorococcales). The main differences between the two phyla are the absence of chlorophyll-b and the absence of starch as an assimilation product in the Xanthophyta. It is therefore understandable that in many species lists the Xanthophyta have been included in the Chlorococcales. A clear example is found in the genus *Tetraedron* (Chlorococcales); many species within this genus have been found to belong to the Xanthophytous genera *Tetraëdriella, Goniochloris* or *Pseudostaurastrum*. In the case of *Tetraedron regulare* Kützing, formely comprising algae with dimensions varying from 10 to 40 µm, the size class 30-40 µm is actually a Xanthophyte: *Tetraedriella regularis* (Kützing) Fott, whereas the smaller algae are still assigned to the Chlorococcales as *Tetraedron regulare* Kützing (see Ettl, 1978 and Komarek & Fott, 1983); the taxonomy of these algae is still confusing for ecological workers.

The identification of *Ophiocytium capitatum* Wolle is doubtful (see Ettl, 1978), since at the moment of identification the right literature was not available and re-examination of the samples did not reveal the characteristics needed for identification. According to Ettl (1978), the correct name must probably have been *Centritractus belenophorus* Lemmermann, a supposition which is born out by a) recent identifications of living material collected from the same sampling localities, b) the fact that I have never encountered very elongated cells, which is the characteristic distinguishing between the Ophiocytiaceae (elongated cells) and the Centritractaceae (cells not elongated), and c) the fact that *Ophiocytium capitatum* tolerates slightly acid environmental conditions. *Centritractus belenophorus* has been found several times in The Netherlands (Dresscher, 1976), but there are probably

many more records of this species under the name of *Ophiocytium capitatum*.

Cryptophyta

The Cryptophyta comprise a wide variety of forms, classified under a few genera which are distinguishable from each other. The algae are sometimes delicate and could be destroyed by rigorous handling. Among the Cryptophyta only members of the genus *Cryptomonas* have been found and only clear representatives of the species *Cryptomonas erosa* and *Cryptomonas ovata* have been recorded as such; the remaining *Cryptomonas*-taxa have been classed under *Cryptomonas* spp.

Pyrrhophyta

Representatives of this phylum have been encountered in small numbers during the entire investigation period at both sampling localities. Especially within the genus *Peridinium* a wide variety of species was found, but it would have taken too much time to identify the species. The genus *Peridiniopsis* Lemmermann comprises the species formerly identified as species of the name *Glenodinium* (Ehrenberg) Stein; even in recent lists the incorrect genus *Glenodinium* is often used (see Bourrelly, 1970).

Chlorophyta

The Volvocales have been identified according to Ettl (1983), with the exception of the genus *Chlamydomonas* Ehrenberg, the taxa of which remained unidentified. The Chlorococcales have been identified according to Komarek & Fott (1983). The taxonomical problems concerning some members of the Chlorococcales have already been mentioned in the discussion of the Cyanobacteria (*Dactylococcopsis* versus *Ankistrodesmus/Monoraphidium*) and the Xanthophyta (*Goniochloris/Tetraëdriella/Pseudostaurastrum* versus *Tetraedron*). But attention should also be drawn to the taxonomic revisions within the genera *Lagerheimia* (incl. *Chodatella*), to *Ankistrodesmus* and its distinction from the genera *Monoraphidium, Selenastrum, Schroederia, Closteriopsis, Chlorolobion* and *Koliella*, to the revisions within the genus *Scenedesmus*, and those within the genus *Crucigenia* (Komarkova-Legnerova, 1969; Komarek, 1974).

In table 11 the taxa encountered in the samples from sampling localities D_1 (open water area) and D_2 (nymphaeid-dominated area) during the entire investigation period have been listed for the algal phyla just discussed (data derived from appendices IIa and b); the number of more frequent taxa (present in more than 10 per cent of the samples) have also been listed in this table.

Table 11. The total number of taxa found in the samples from pond D of the Oude Waal (October 1978 - November 1979).
Left columns: all taxa encountered; right columns: only those taxa included that were present in at least 10 % of the 48 samples from the locality concerned. D_1: open water area; D_2: nymphaeid-dominated area.

			in more than 10 % of the 48 samples	
	D_1	D_2	D_1	D_2
Cyanobacteria	5	4	-	-
Xanthophyta	6	6	4	4
Cryptophyta	3	3	3	2
Pyrrhophyta	4	4	4	3
Euglenophyta	20	17	12	12
Chlorophyta	103	96	49	51
Total	141	130	72	72

At D_1 the following taxa have been found, which were not found at D_2: *Oscillatoria agardhii, Phacus pusillum, Phacus triqueter, Trachelomonas caudata, Planktosphaeria gelatinosa, Pediastrum integrum, Lagerheimia longiseta, Chlorolobion braunii, Scenedesmus arcuatus* var. *capitata, Scenedesmus hystrix, Scenedesmus linearis, Scenedesmus serratus, Scenedesmus velitaris* and *Crucigeniella apiculata*. The following taxa have been found at D_2 and not at D_1: *Closterium moniliferum, Spyrogyra* spp. and *Oedogonium* spp..

Taking into account the 10 per cent presence level the following taxa were present at D_1 and were rare at D_2: *Cryptomonas ovata, Ceratium hirundinella, Pteromonas aculeata, Ankyra ancora, Schroederia spiralis, Chlorella* spp., *Scenedesmus obtusus* f. *obtusus* and *Scenedesmus opoliensis*, whereas the following taxa were present at D_2, but did not play a role of any importance in D_1: *Closteriopsis longissima, Kirchneriella lunaris, Quadrigula closterioides, Willea irregularis, Crucigenia fenestrata, Scenedesmus denticulata, Scenedesmus longispina* and *Scenedesmus spinosus*.

6.1.2. Chrysophyta and Prymnesiophyta (Haptophyta)

Within the phytoplankton as a whole Chrysophyta and Prymnesiophyta occupy an important place as far as their biomass and the number of species are concerned (table 12). The Chrysophyta and Prymnesiophyta encountered in the samples are taxonomically arranged as indicated in appendix IIIa

Table 12. Species composition and mean annual biomass of the phytoplankton in pond D of the Oude Waal.
D_1: open water area; D_2: nymphaeid-dominated area.

taxa	D_1	D_2	biovolume	D_1	D_2
Chlorophyta	34 %	32 %	Bacillariophyta	25 %	30 %
Bacillariophyta	29 %	34 %	Cryptophyta	23 %	26 %
Chrysophyta/ Prymnesiophyta	25 %	23 %	Chlorophyta	20 %	16 %
			Chrysophyta/ Prymnesiophyta	17 %	15 %
Euglenophyta	7 %	6 %			
Xanthophyta	2 %	2 %	Euglenophyta	10 %	7 %
Cyanobacteria	2 %	1 %	Pyrrhophyta	5 %	4 %
Cryptophyta	1 %	1 %	Xanthophyta	1 %	1 %
Pyrrhophyta	1 %	1 %	Cyanobacteria	0 %	1 %

(according to Ettl, 1980; Bourrelly, 1981; Round, 1981; Preisig & Hibberd, 1983).

A number of species among the Chrysophytes have a lorica made of pectic, cellulosic, siliceous or calcareous substances. As far as its construction is concerned the lorica could be of two types: 'true lorica' and 'scaly lorica'. Representatives of species having a true lorica are shown in fig. 24, of those having a scaly lorica in fig. 25.

As early as 1929, Korshikov was able to distinguish 5 species within the genus *Synura*, solely on the basis of the ultrastructure of their scales. His observations were made with air-dried specimens using a light microscope. Since 1955 the use of transmission electron microscopy (TEM) was introduced in the study of the taxonomy of the scale-bearing Chrysophytes (Asmund, 1955; Fott, 1955; Manton, 1955). But it took a long time before ecological investigators also started to apply TEM for the taxonomical part of their studies, partly because of the costs associated with it and partly because of extra handling. Up to 1976, no records of scale-bearing Chrysophytes and Prymnesiophytes, supported by TEM-observations, are known from The Netherlands. Since Wujek & van der Veer (1976), numerous species have been recorded, the majority of which were new to The Netherlands (Roijackers,1981b, 1981c,Roijackers & Kessels, 1981; Roijackers, in press.; Roijackers & Kessels, in press.).

Genera of which the species can only be identified correctly with the help of TEM are: *Mallomonopsis*, *Mallomonas*, *Synura*, *Chromophysomonas*, *Chrysosphaerella*, *Paraphysomonas*, *Polylepidomonas*, *Hymenomonas* and some

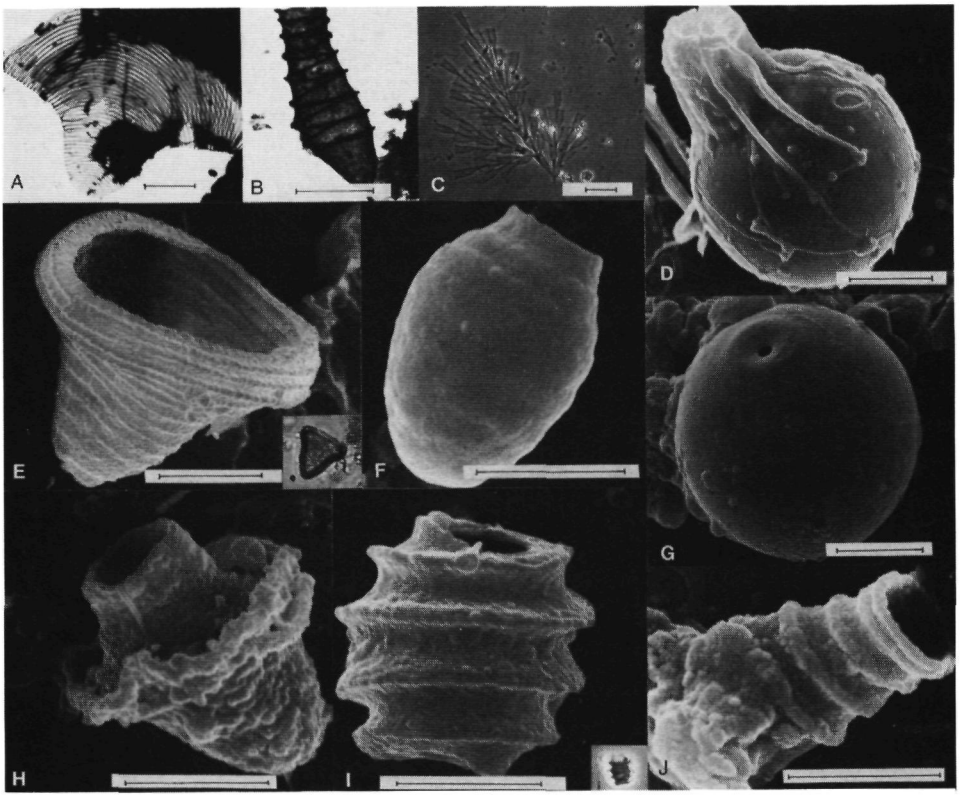


Fig. 24. Chrysophytes with a true lorica. A: Bicocoeca crystallina (TEM); B: Dinobryon suecicum (TEM); C: D. divergens: colony (LM; Ph); D: D. divergens: cyst (SEM); E: Bicocoeca planktonica (SEM) and e: B. planktonica (LM;Ph); F: Kephyrion/Pseudokephyrion spec. (SEM); G: Chrysococcus spec. (SEM); H: Stenokalyx monilifera (SEM); I: Kephyrion spirale (SEM) and i: K. spirale (LM; Ph); J: Pseudokephyrion klarmetii (SEM).
TEM = transmission electron microscope. SEM = scanning electron microscope; LM = light microscope; Ph = phase-contrast.
The bars indicate 5 µm, in fig. D the bar indicates 50 µm.

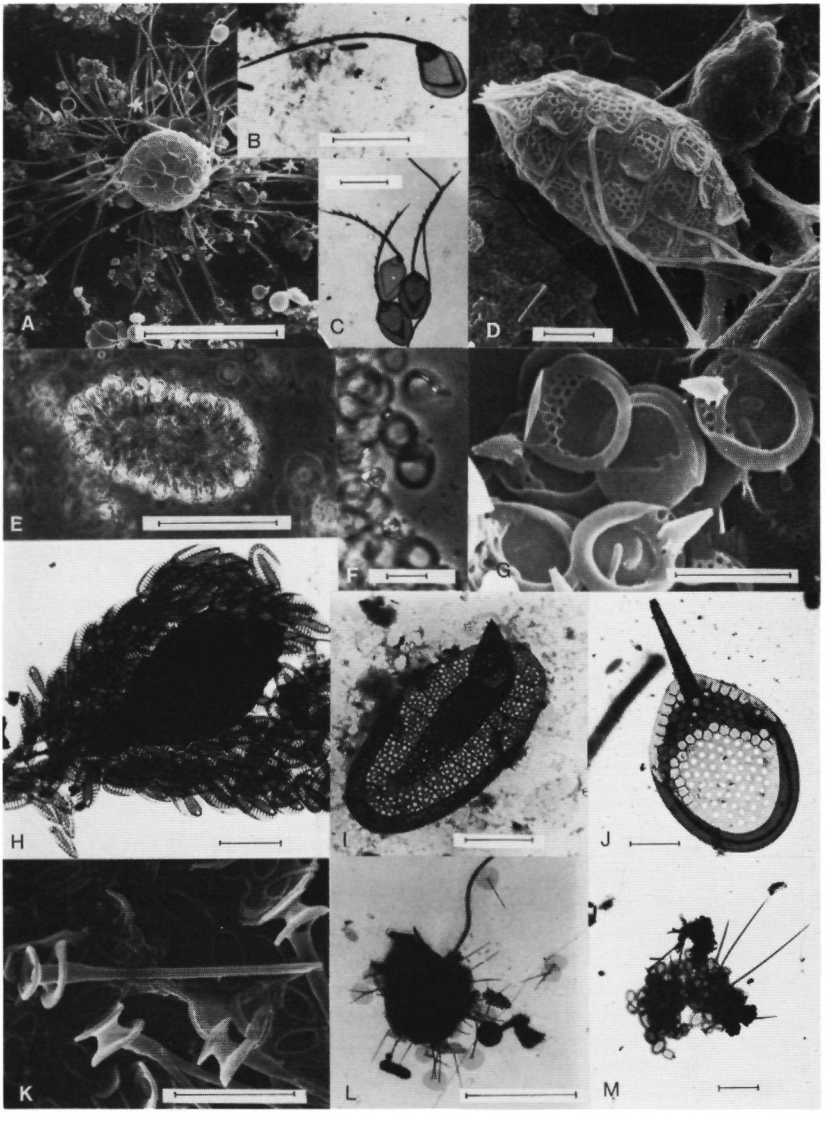


Fig. 25. Chrysophytes with a scaly lorica. A: Mallomonas caudata (SEM); B: M. monograptus: scale with bristle (TEM); C: M. acaroides: scales with bristles (TEM); D: M. punctifera (SEM); E: Synura spec.: colony (LM; Ph); F: S. uvella: scales (LM; Ph); G: S. uvella: scales (SEM); H: S. petersenii: cell with scales (TEM); I: S. petersenii: scale (TEM); J: S. spinosa: scale (TEM); K: Chrysosphaerella brevispina: scales and spines (SEM); L: Paraphysomonas imperforata: cell with spines (TEM); M: Chromophysomonas trioralis: cel with scales and spines (TEM).
TEM = transmission electron microscope; SEM = scanning electron microscope; LM = light microscope; Ph = phase-contrast.
The bars indicate 5 µm, in figs. A and E thebars indicate 50 µm and in figs. I and J the bars indicate 1 µm.

species of *Bicoecea*. Nevertheless some species within these genera can easily be identified without the use of an electron microscope, e.g. *Mallomonas akrokomos*, *M. acaroides*, *M. tonsurata* and *M. caudata*; these species could thus be included in the appendices IIa and b.

For the other genera the use of the electron microscope is superfluous, as it does not provide any extra information useful for the identification of the organisms in question.

The Chrysophytes and Prymnesiophytes encountered in the samples from D_1 (open water area) and D_2 (nymphaeid-dominated area) have been listed in table 13 and 14 respectively.

Some taxa require some additional remarks:

Chrysococcus spp.

The delineation of the species in question is not clear. In most specimens the lorica possesses two pores, but specimens with one pore have also been found (*C. rufescens*). For the taxa which possess two pores, the differences between the three species concerned are too small to be taken into account in a routine programme. Fig. 26 gives an example which illustrates the presence of more than one species of the genus *Chrysococcus* in the sample. In this figure the number of specimens is given for each lorica diameter measured. Two to three diameter classes could be distinguished and the four species concerned (*C. minutus*, *C. porifer*, *C. biporus* and *C. rufescens*) have been indicated in this figure.

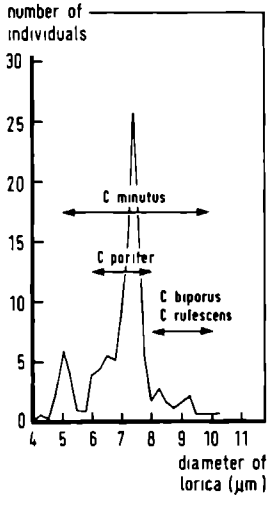


Fig. 26. The number of Chrysococcus spp. specimens as a function of the diameter of the lorica. The sample was taken from locality D_1 (open water area) of pond D of the Oude Waal at January 29. 1979.

Table 13. The presence of Chrysophyte and Prymnesiophyte taxa in the samples taken from sampling locality D_1 (open water area) in pond D of the Oude Waal in the period October 1978 to November 1979.
Only those taxa have been included which were present in more than 10 % of the 47 samples. Frequency classes as in table 9.
1 = rare; 2 = common; 3 = abundant; x = abundance not estimated.

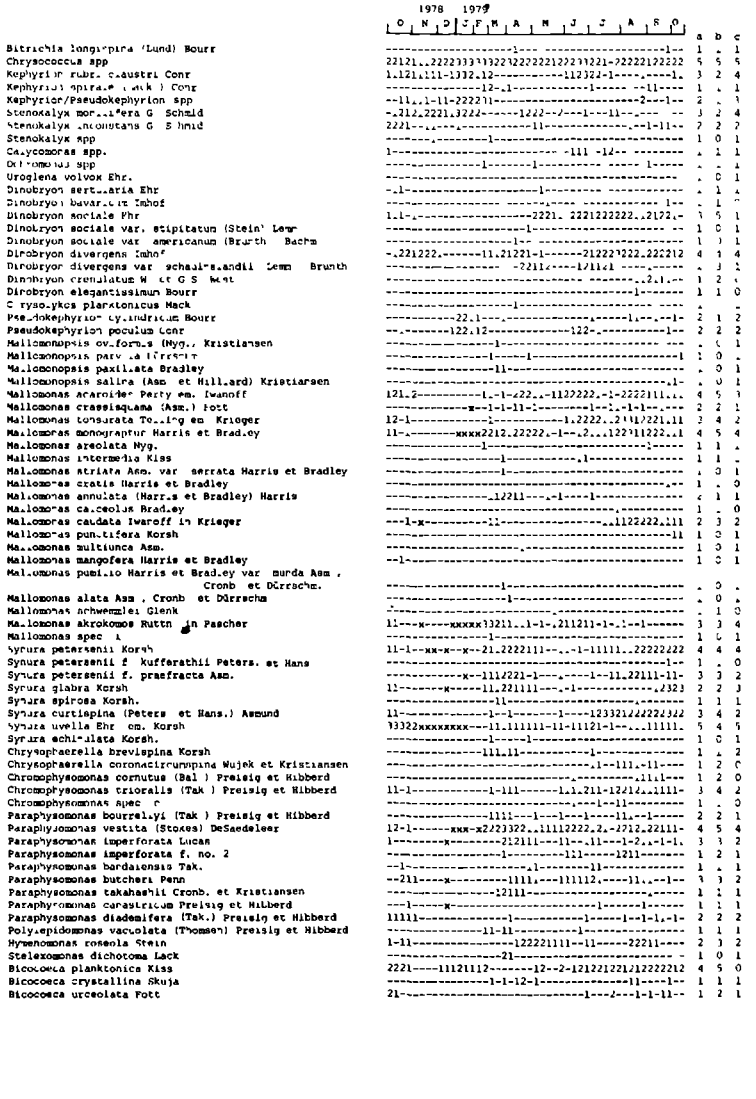


Table 14. The presence of Chrysophyte and Prymnesiophyte taxa in the samples taken from sampling locality D_2 (nymphaeid-dominated area) in pond D of the Oude Waal in the period October 1978 to November 1979. Only those taxa have been included which were present in more than 10 % of the 47 samples. Frequency classes as in table 9. 1 = rare; 2 = common; 3 = abundant; x = abundance not estimated.

	1978 1979 O N D J F M A M J J A S O	a	b	c
Bitrichichia longispina (Lund) Bourr.	----------1----1----------	1	1	1
Chrysococcus spp.	22:2111222231111122322221-21211221222232222222	5	5	5
Kephyrion rubri-claustri Conr.	11121-111-1322112---------11232211----2------	3	2	3
Kephyrion spirale (Lack.) Conr.	----------112-11----------	1	0	1
Kephyrion/Pseudokephyrion spp.	--111-1111-2222-1----------2111121-	2	2	3
Stenokalyx monilifera G. Schmidt	-112211221132223-----12221-2----2-11----------	3	2	4
Stenokalyx inconstans G. Schmidt	1221-------1---------11---- -------111-1-111-	2	2	2
Stenokalyx spp.	----------	1	0	1
Calycomonas spp.	----------2111-12---1-----11-	1	2	1
Ochromonas spp.	----------1----------	1	1	0
Uroglena volvox Ehr.	----------1	1	0	1
Dinobryon sertularia Ehr.	1121-1----------12----------	1	1	1
Dinobryon sociale Ehr.	11-111----------22121-222-112712122222	3	5	2
Dinobryon sociale var. stipitatum (Stein) Lemm.	----------1----------	1	0	1
Dinobryon sociale var. americanum (Brunth.) Bachm.	----------1----------1----------	1	1	1
Dinobryon divergens Imhof	11221221-------11121221-1------1122222221212212	4	4	4
Dinobryon divergens var. schauinslandii (Lemm.) Brunth.	----------22111----12--11----------	1	2	1
Dinobryon crenulatum W. et G.S. West	----------1-2111--	1	2	0
Chrysolykos planktonicus Mack	----------1----------	1	0	1
Pseudokephyrion cylindricum Bourr.	----------2111---1----------1--1----------	1	1	1
Pseudokephyrion poculum Conr.	-------11-122111---------12-1---------11-1	2	2	2
Mallomonopsis oviformis (Nyg.) Kristiansen	----------1----------	1	0	1
Mallomonopsis parvula Dürrschm.	----------1----------	1	0	1
Mallomonopsis paxillata Bradley	----------11----------	1	0	1
Mallomonopsis salina (Asm. et Hilliard) Kristiansen	----------1-	1	0	1
Mallomonas acaroides Perty em. Iwanoff	1211--x-----xx11-1-222111-1122221---1212-11111	4	4	3
Mallomonas crassisquama (Asm.) Fott	-1----------1-1-11-1--1-----1---2-1-111--1-	2	2	2
Mallomonas tonsurata Teiling em. Krieger	12111----------1----------1-122221122212221111	3	4	2
Mallomonas monograptus Harris et Bradley	1111---------xx22121222221-1--12111121212222111	4	5	4
Mallomonas intermedia Kiss.	----------11----------	1	1	0
Mallomonas striata Asm. var. serrata Harris et Bradley	----------1----------	1	0	1
Mallomonas cratis Harris et Bradley	----------1-1--1-	1	1	1
Mallomonas annulata(Harris et Bradley) Harris	-------x---------112211------1--1----------	1	1	2
Mallomonas caudata Iwanoff in Krieger	-1---------x----11----------111-122221111	2	3	2
Mallomonas punctifera Korsh.	----------111	1	0	1
Mallomonas multiunca Asm.	----------1----------	1	0	1
Mallomonas mangofera Harris et Bradley	-------x----------	1	0	1
Mallomonas pumilio Harris et Bradley var. munda Asm., Cronb. et Dürrschm.	----------1----------	1	0	1
Mallomonas alata Asm., Cronb. et Dürrschm.	----------1----------	1	0	1
Mallomonas akrokomos Ruttn. in Pascher	--11--x--x-xxxx3321111-1112111-1-------1--1----	3	3	4
Mallomonas spec. 1	----------1----------	1	0	1
Synura petersenii Korsh.	11-1--xx--x-x-x21122221l1--1--11111---122222222	4	4	4
Synura petersenii f. praefracta Asm.	-------x------1112221-1---1-----1-1--21111-11-	2	3	2
Synura glabra Korsh.	---1------x----1112211111--------1---------11223	2	2	3
Synura spinosa Korsh.	----------11----------1----------	1	1	1
Synura curtispina (Peters. et Hans.) Asm.	11----------1---1----------12112122223321	2	3	2
Synura uvella em. Korsh.	33322xxxxxxxx-x1111111111-11-11121-11-111111111	5	4	5
Synura echinulata Korsh.	----------1-----1----------	1	0	1
Chrysophaerella brevispina Korsh.	----------11111----------	1	0	1
Chrysophaerella coronacircumspina Wujek et Kristiansen	----------1--11-1-1-----	1	2	0
Chromophysomonas cornutus (Bal.) Preisig et Hibberd	----------11---------111----	1	2	0
Chromophysomonas triloralis (Tak.) Preisig et Hibberd	1--1----------1-111------11111111-2212121-1--	3	4	2
Paraphysomonas bourrellyi (Tak.) Preisig et Hibberd	----------x-1-1-----1---1-1-1-1---11-11-1---	2	3	1
Paraphysomonas vestita (Stokes) DeSaedeleer	11-1--x---xxx-x2223322111--12232121-22121111-1-	4	5	4
Paraphysomonas imperforata Lucas	----------2121111---22-1111---1-111-1---1	2	3	2
Paraphysomonas imperforata f. no. 2	----------1---------1121111-22-1-------	2	3	1
Paraphysomonas bandaiensis Tak.	--11----------11---------1----------	1	1	1
Paraphysomonas butcheri Penn.	--111----------11111----221111----1111-1--	2	3	2
Paraphysomonas takahashii Cronb. et Kristiansen	----------12111------1---------1-----	1	1	1
Paraphysomonas diadesmifera (Tak.) Preisig et Hibberd	11211x----------1---------11----------	1	1	2
Paraphysomonas species c	----------1----------	1	1	0
Polylepidomonas vacuolata (Thomsen) Preisig et Hibberd	----------1-11---------11---------1--1--	1	1	1
Hymenomonas roseola Stein	1111----------122221111--12------22211----	3	3	2
Hymenomonas species a	---1----------1----------	1	0	1
Stelexomonas dichotoma Lack.	----------21----------	1	0	1
Bicoececa planktonica Kiss.	22211---1--11111------12111222221222121212221	4	5	3
Bicoececa crystallina Skuja	--1----------1-1-12-1------2-----1---11-----	2	2	1
Bicoececa urceolata Pott	21----------11--11--2-1-111-	2	2	1

Kephyrion, Stenokalyx and *Pseudokephyrion*

These three genera enclose a group of true-loricate Chrysophytes with a typical large opening and a wide range of lorica forms. The organisms are not sessile. Bourrelly (1957, 1981) places the genus *Stenokalyx* in the genus *Kephyrion* as he considered the few characteristic differences between both genera to be of less importance than for instance Fott (1959, 1964) had stated. Because of the clear distinctive ornamentation of the lorica I will use the name *Stenokalyx*, thus clearly delimitating the two different groups of taxa.

The distinction between the two genera *Kephyrion* and *Pseudokephyrion* is based on the possession of just one flagellum or two flagellae respectively. It is obvious that in a number of situations this distinctive character was not detectible, particularly as the lorica is usually coloured. Hence in those situations in which the species could not be identified the organisms have been indicated as *Kephyrion/Pseudokephyrion* spp..

Out of the complete species list of Chrysophyta and Prymnesiophyta it was found that 74 taxa occurred at D_1 (open water area) and 68 taxa at D_2 (nymphaeid-dominated area) (data covering the entire investigation period); 66 taxa were present at both sampling localities. The taxa present at one sampling locality only, have been encountered only once and must be regarded as accidental. Only *Paraphysomonas canistrum* seems to have a clear prevalence for the open water area, since the species has been found there four times during the sampling period. Even if only those taxa were taken into account which occurred in at least 10 per cent of the samples (42 taxa at D_1 and 43 taxa at D_2) clear differences could still not be observed. Only *Dinobryon sertularia*, generally known as a typical euplanktonic species, is found to occur more often at sampling locality D_2 (nymphaeid-dominated area).

In fig. 27 the biovolume development of some Chrysophytes is given as a function of time.

6.1.3. Bacillariophyta (Diatoms)

The Bacillariophyta are the most important algae among the phytoplankton of the Oude Waal both in terms of biovolume and number of taxa (table 12). The taxonomical arrangement of the Bacillariophyta encountered in the samples is given in appendix IIIb (according to Ettl, 1980; Bourrelly, 1981; Round, 1981).

Among the phytoplankton groups the Bacillariophyta have the longest

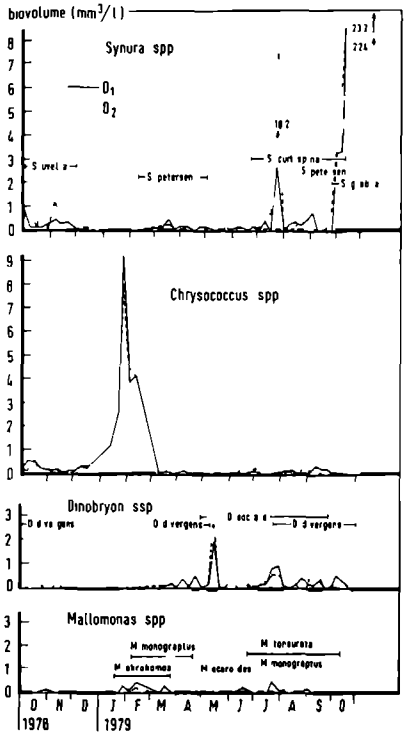


Fig. 27. Biovolume development as a function of time for some Chrysophytes from pond D of the Oude Waal. D_1 = open water area; D_2 = nymphaeid-dominated area.

history as regards the recording of correctly identified taxa. Since the specific methods for identifying Diatoms involve the preparation of permanent slides, the necessity of an immediate examination of living material, which takes a great deal of time, is removed, and the slides could be examined later at a more convenient time. Nevertheless, numerous problems in the identification of Diatoms still remain to be solved and identification of the taxa is not always possible. Only those species that could be identified correctly without the use of permanent slides have been included in the appendices IIa and b. Since several species could not be identified, only their generic names have been given in these lists.

Bacillariophyta encountered in the samples from D_1 (open water area) and D_2 (nymphaeid-dominated area), and identified by means of permanent slides, have been listed in table 15 and 16 respectively.

Some of the taxa require some additional taxonomic remarks as the species lists are not always directly comparable to other species lists:

Table 15. Presence of Bacillariophyte taxa in the samples taken from sampling locality D_1 (open water area) in pond D of the Oude Waal in the period October 1978 to November 1979.
Only those taxa have been included which were present in more than 10 % of the 48 samples. Frequency classes as in table 9.
1 = occasional hit, 1-3 individuals per slide; 2 = 4-10 individuals; 3 = more than 10 individuals, not dominant; 4 = as 3, but dominant; 5 = mass occurrence.

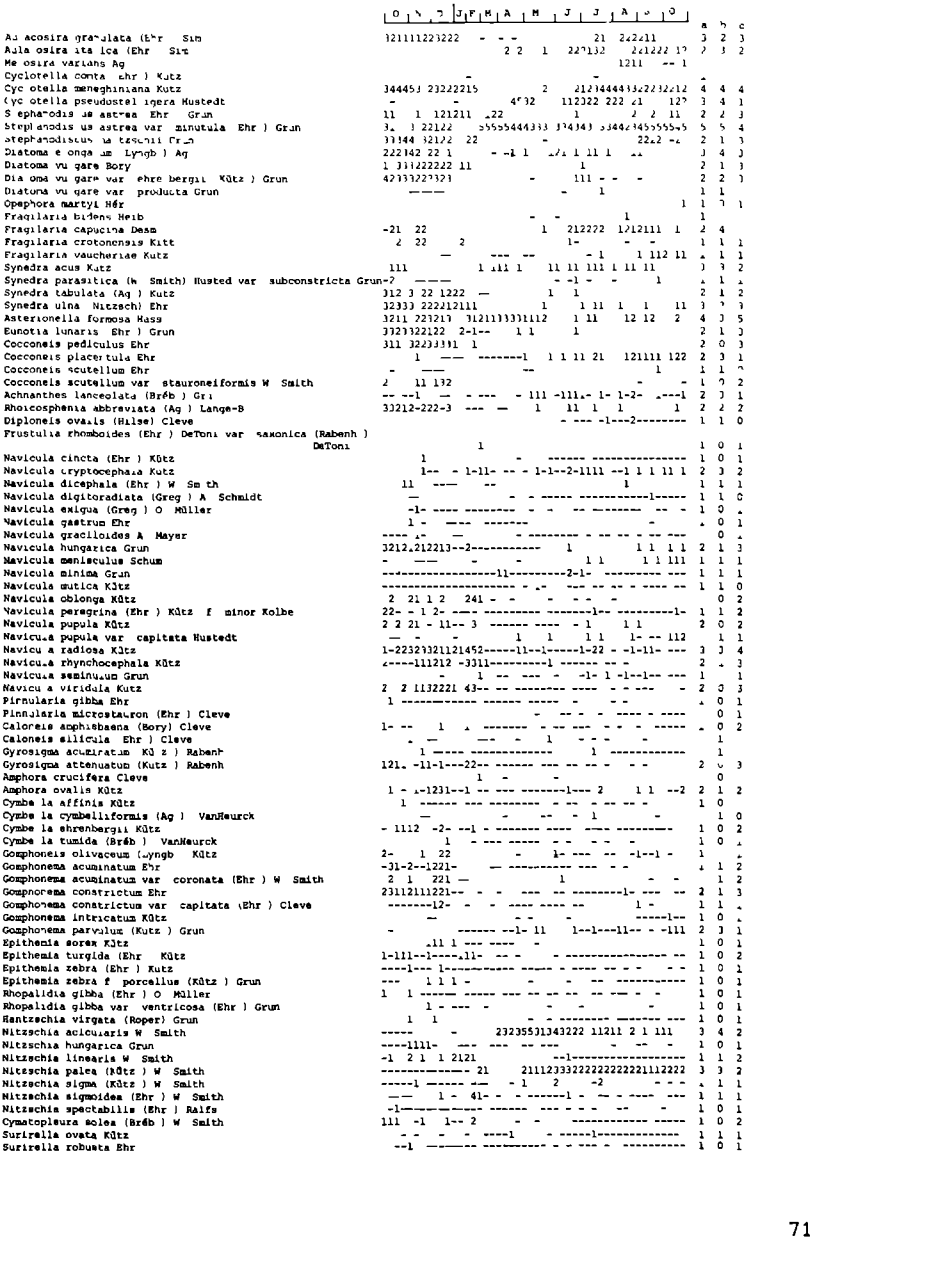
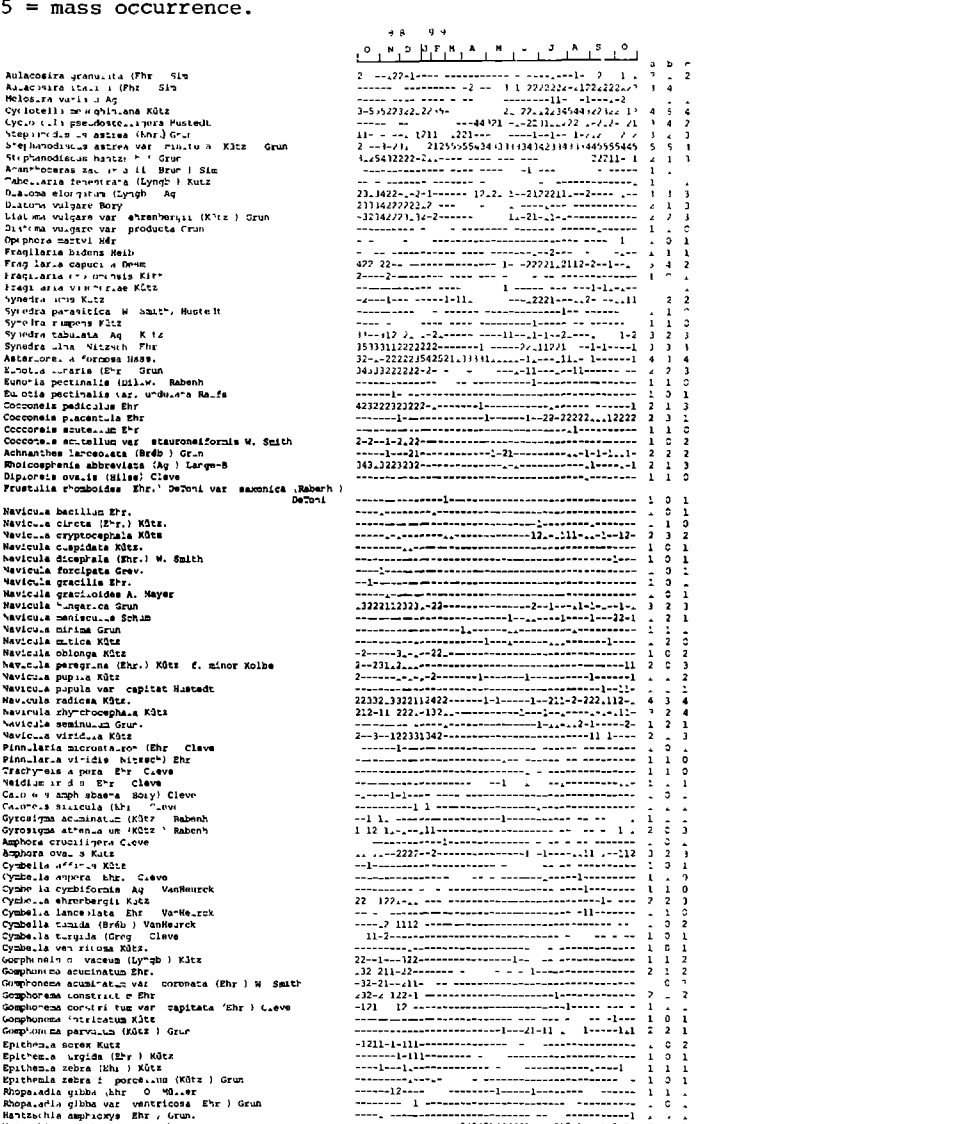


Table 16. Presence of Bacillariophyte taxa in the samples taken from sampling locality D_2 (nymphaeid-dominated area) in pond D of the Oude Waal in the period October 1978 to November 1979.
Only those taxa have been included which were present in more than 10 % of the 48 samples. Frequency classes as in table 9.
1 = occasional hit, 1-3 individuals per slide; 2 = 4-10 individuals; 3 = more than 10 individuals, not dominant; 4 = as 3, but dominant; 5 = mass occurrence.



Melosira and *Aulacosira*

The delineation of the *Melosira*-group against the genus *Cyclotella* (Nagumo & Kobayasi, 1977) and against the genus *Stephanodiscus* (Round, 1972) is sometimes highly problematic. But even within the *Melosira*-group itself ultrastructural differences between taxa have led to the distinction of two genera within the former genus *Melosira*, namely *Melosira* and *Aulacosira* (Simonsen, 1979).

Cyclotella and *Stephanodiscus*

According to Round (1970) the distinction between these two genera is difficult and the ultrastructure of the diatom frustules should be taken into account.

Acanthoceras

Recently Simonsen (1979) has reinstated *Attheya zachariasi* in the genus *Acanthoceras*.

Rhoicosphenia

The species *Rhoicosphenia curvata* has been studied by Lange-Bertalot (1980a)with an electron microscope in order to determine its taxonomical position. According to his studies the species name should be *R. abbreviata*.

Gomphoneis and *Gomphonema*

Dawson (1974) showed that some species within the genus *Gomphonema* should be placed in the genus *Gomphoneis*, for instance *G. olivaceum*.

Navicula and *Nitzschia*

Some of the smaller species have to be studied with an electron microscope to establish the species name (Lange-Bertalot, 1976/1977, 1978, 1980b; Lange-Bertalot & Simonsen, 1978).

Fig. 28 gives photographs of some of the taxa mentioned above.

On a round-the-year basis 87 taxa have been found in the samples from D_1 (open water area) and 101 taxa in those from D_2 (nymphaeid-dominated area). Among these taxa only *Neidium iridis* and *Nitzschia dissipata* cannot have been accidental hits, as both species have been found several times - during the period of maximal development of the nymphaeids - at D_2, and never at D_1. Taking into account only those taxa which were present in at least 10 per cent of the samples, it is found that 50 taxa were present at D_1 and 55 taxa at D_2; of these taxa 5 were morefrequently found at D_1, whereas 10 were more frequently found at D_2. Of these 5 taxa *Fragilaria crotonensis* , but also *F. vaucheriae* and to a lesser extent *Navicula pupula* var. *capitata* appeared

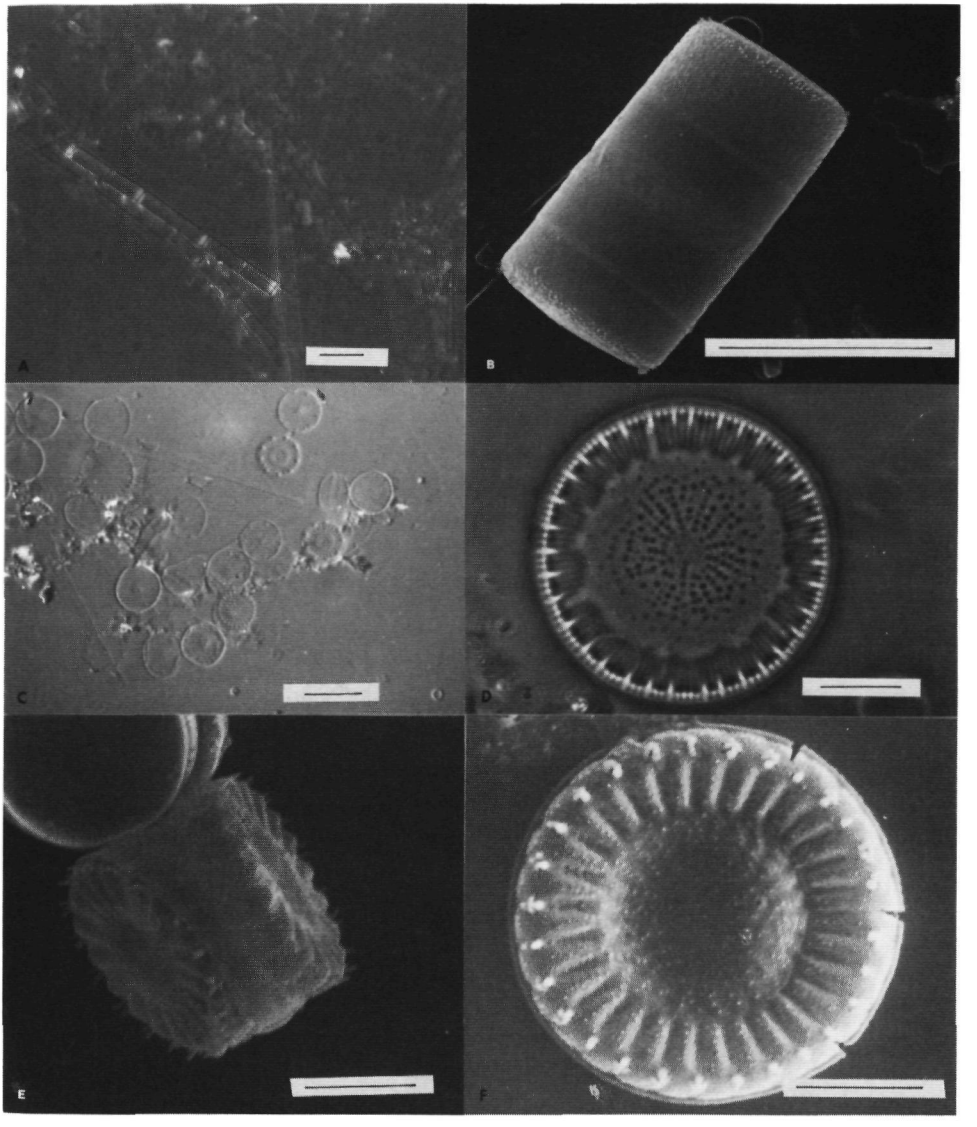


Fig. 28. Diatoms. A. Aulacosira granulata (LM; Ph); B. Melosira varians (SEM); C: Cyclotella pseudostelligera and Stephanodiscus hantzschii (LM; DIC); D: Cyclotella comta (LM; Ph); E and F: C. meneghiniana (SEM). TEM = transmission electron microscope; SEM = scanning electron microscope; LM = light micrscope; Ph = phase-contrast; DIC = differential interference contrast. The bars indicate 10 µm.

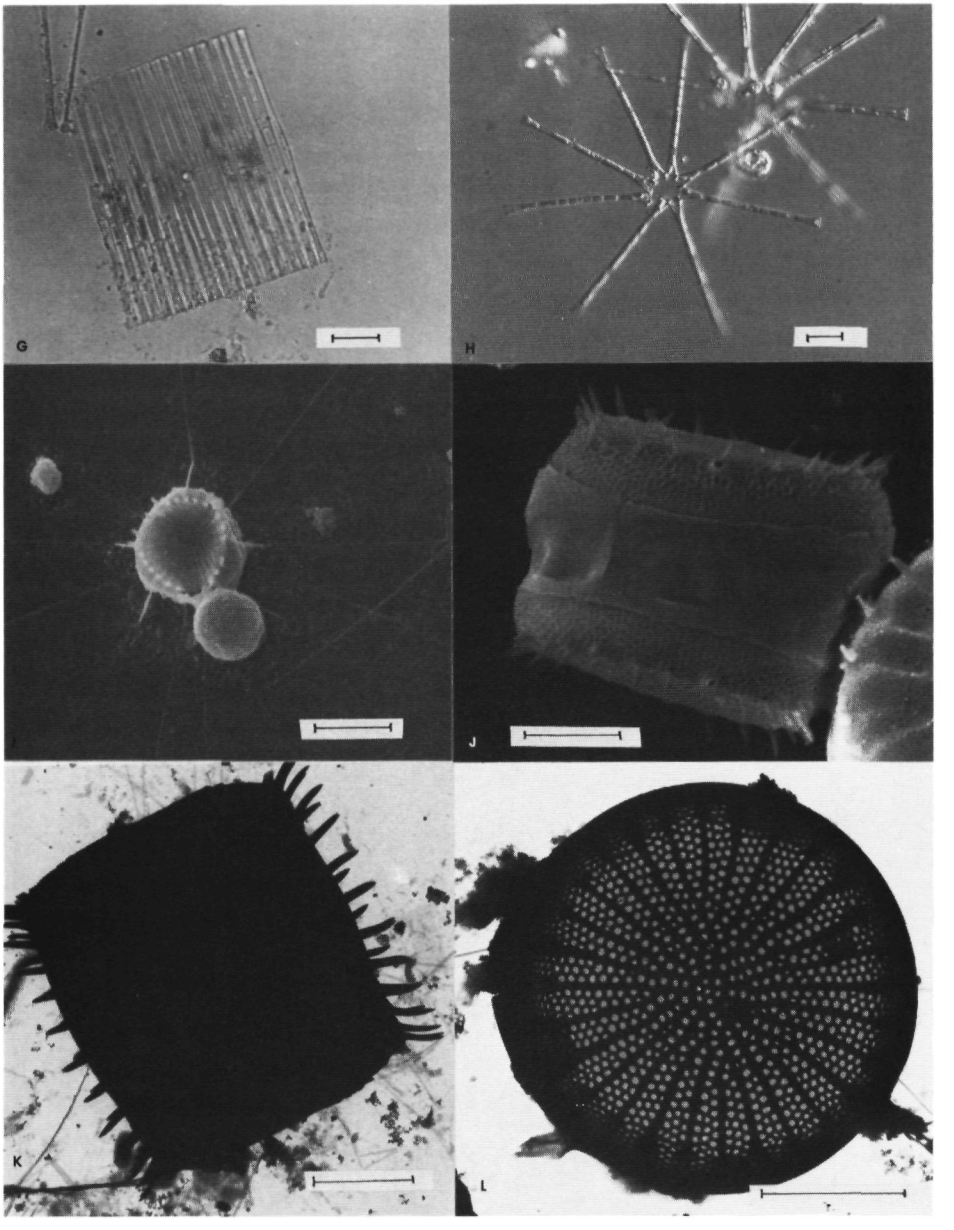


Fig. 28. (continue). G: Fragilaria crotonensis (LM); Asterionella formosa (LM; DIC); I to L: Stephanodiscus hantzschii (I and J: SEM; K and L: TEM).
TEM = transmission electron microscope; SEM = scanning electron microscope; LM = light micrsocope; DIC = differential interference microscope.
The bars indicate 10 µm.

to develop all of their major populations at D_1 in the period after the disappearance of the aboveground biomass of the nymphaeids at D_2. Among the frequent taxa better represented at D_2 than at D_1 *Cymbella tumida*, *Gomphonema constrictum* var. *capitata* and *Epithemia sorex* especially, and to a lesser extent also *Nitzschia sigmoidea*, appeared to develop their major populations at D_2; these species too were found in samples taken after the major development period of the nymphaeids.

To illustrate not only the qualitative but also the quantitative importance of some Diatoms, fig. 29 shows the biovolume of some characteristic taxa, plotted against time.

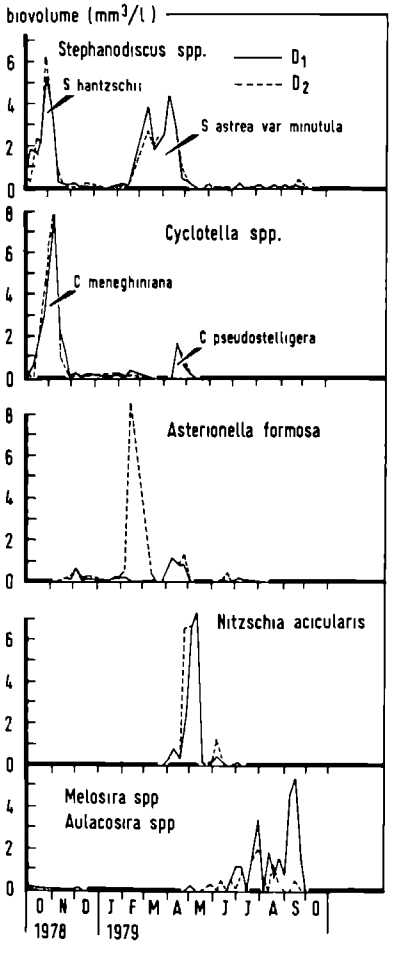


Fig. 29. Biovolume of some Bacillariophyta (Diatoms) as a function of time in samples from pond D of the Oude Waal.

6.1.4. The nannophytoplankton species composition

Various authors have introduced prefixes to categorize the phytoplankton according to the individual sizes of the organisms. In this connection special attention has been paid to the nannoplankton (Rodhe et al., 1958; Yentsch & Ryther, 1959; Fogg & Belcher, 1961; Wetzel, 1964). The nannoplankton size fraction, however, is interpreted differently by various authors. Pavoni (1963) used 30 µm as the upper limit of the nannoplankton fraction; Nauwerck (1963) put the limit at 80 µm, Kalff (1972) at 64 µm, Gliwicz & Hillbricht-Ilkowska (1972) at 50 µm and Manny (1972) even at 10 µm.

In this study nannophytoplankton is taken to mean the phytoplankton fraction not retained by a plankton net with 30 µm meshes.

The species composition of the nannophytoplankton subcommunities is quite different from that of the total phytoplankton communities of which they form a substantial part. Table 17 shows that all the Cryptophyte taxa have been included in the nannophytoplankton as well as over 90 % of the Chlorophyte taxa (almost all Chlorococcal algae). Considering only the nannophytoplanktonic algae at the sampling localities, most taxa are found among the Chlorophyta (over 50 %) and the Chrysophyta (25 %). The number of taxa at sampling localities D_1 (open water area) and D_2 (nymphaeid-dominated area) is given in table 18 for each phylum. The total number of nannophytoplanktonic taxa is about 55 % of the total number of the total phytoplankton. Considering only the frequent taxa (present in more than 10 % of the samples), about 60 % is found among the nannophytoplankton fraction.

Differences in the nannophytoplankton species composition for sampling localities D_1 and D_2 are very small.

Table 17. A. Species composition and mean annual biomass of the nannophytoplankton of pond D of the Oude Waal.
B. Percentage of the total phytoplankton species composition and annual biomass of the nannophytoplankton fraction.
D_1 = open water area; D_2 = nymphaeid-dominated area.

taxa	A D_1	A D_2	B D_1	B D_2	biovolume	A D_1	A D_2	B D_1	B D_2
Chlorophyta	55 %	53 %	92 %	91 %	Bacillariophyta	19 %	23 %	60 %	54 %
Bacillariophyta	10 %	12 %	21 %	20 %	Cryptophyta	22 %	26 %	71 %	75 %
Chrysophyta/ Prymnesiophyta	25 %	24 %	58 %	59 %	Chlorophyta	17 %	17 %	64 %	64 %
					Chrysophyta/ Prymnesiophyta	21 %	15 %	94 %	92 %
Euglenophyta	5 %	4 %	40 %	41 %					
Xanthophyta	1 %	1 %	33 %	33 %	Euglenophyta	16 %	13 %	94 %	92 %
Cyanobacteria	1 %	1 %	40 %	50 %	Pyrrhophyta	6 %	6 %	71 %	63 %
Cryptophyta	2 %	2 %	100 %	100 %	Xanthophyta	0 %	0 %	14 %	13 %
Pyrrhophyta	2 %	2 %	75 %	75 %	Cyanobacteria	0 %	1 %	0 %	26 %

Table 18. Total number of taxa in the nannophytoplankton fraction of pond D of the Oude Waal.
D_1 = open water area; D_2 = nymphaeid-dominated area.

	all taxa encountered		in more than 10% of the samples	
	D_1	D_2	D_1	D_2
Cyanobacteria	2	2	-	-
Chrysophyta/ Prymnesiophyta	43	40	29	28
Bacillariophyta	18	20	14	15
Xanthophyta	2	2	2	2
Cryptophyta	3	3	3	2
Pyrrhophyta	3	3	-	-
Euglenophyta	8	7	5	5
Chlorophyta	95	87	44	46
Total	174	164	97	98

6.2. BIOMASS DEVELOPMENT

The term 'phytoplankton biomass' should only refer to the living algal material present in a unit area at a given time (Westlake, 1965). The biomass of phytoplankton can be expressed in several ways (Vollenweider, 1974). This is largely due to the fact that it is impossible to separate the algal cells from the other seston components (tripton, zooplankton). In my studies the following three biomass characteristics were chosen a) biovolume, b) dry weight and ash-free dry weight and c) chlorophyll-a. Each method has its advantages and disadvantages, which will be evaluated in the appropriate sections. The choice of these three biomass methods was determined by available laboratory facilities rather than by strictly theoretical considerations.

Much has been said about the advantages and disadvantages of the three biomass determination methods, and many workers have compared the results of various methods in terms of correlations (Iwamura et al., 1975; LeBorgne, 1975a, 1975b; Paerl et al., 1976; Hallegraeff, 1976, 1977; Karlström & Backlund, 1977). In the present study, however, it was attempted to combine information about the structure of the phytoplankton biomass obtained via the three different lines of approach represented by the three different biomass methods, which were applied to the same phytoplankton communities.

6.2.1. Biovolume

Among the phytoplankton biomass determination methods the determination

of the biovolume is the only one that reflects directly upon the species themselves. Therefore, although the method is highly laborious it provides direct information about the species involved and is thus the best of all phytoplankton biomass determination methods if the structure within the phytoplankton communities is to be revealed. Due to the fact that only a limited number of subsamples can be counted, large statistical errors are involved (Lund et al., 1958; Kutkuhn, 1958), errors which can in some cases be as high as 12 % (Hallegraeff, 1976, 1977).

The biovolume of the total phytoplankton as a function of time at sampling localities D_1 (open water area) and D_2 (nymphaeid-dominated area) is shown in fig. 30; the same has been done for the biovolume of the nannophytoplankton

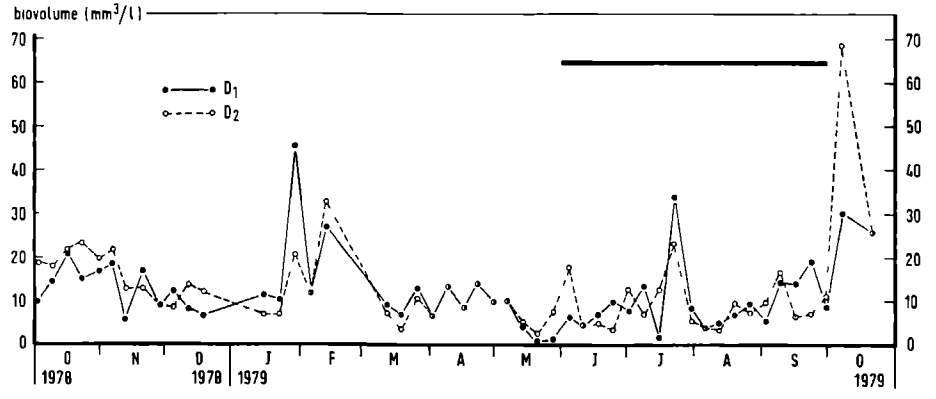


Fig. 30. The biovolume of the total phytoplankton as a function of time in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated.

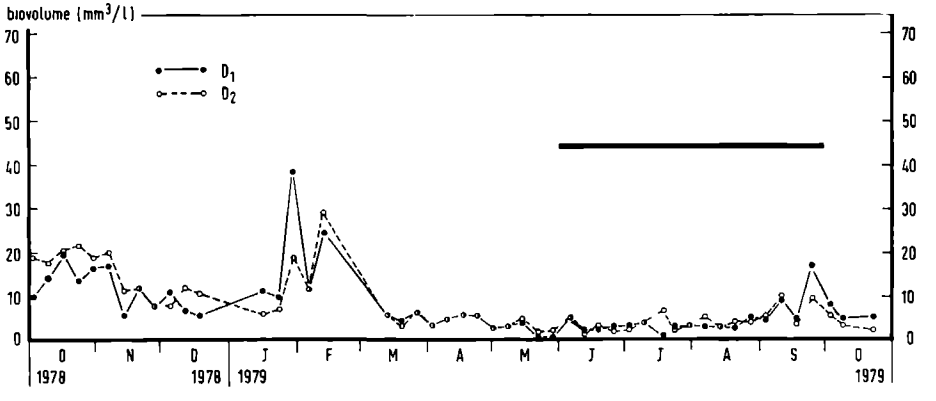


Fig. 31. As fig. 30. The biovolume of the nannophytoplankton as a function of time in pond D of the Oude Waal.

D_1 = open water area; D_2 = nymphaeid-dominated area.

in fig. 31. The percentual contribution to the total biovolume of the various phytoplankton groups is represented as a function of time in figs. 32 and 33 for D_1 (open water area) and D_2 (nymphaeid-dominated area) respectively. Figs. 34 and 35 show the same for the nannophytoplankton biovolume at D_1 and D_2 respectively. Some examples of the development of the biovolume of some characteristic taxa in the course of the year have already been given in sections 6.1.2. and 6.1.3. The importance of the various phyla as reflected by their percentual contribution to the mean annual biovolume is shown in table 12 for the total phytoplankton and in table 17 for the nannophytoplankton. Fig. 36 shows the frequency distribution for the 8 major algal groups, based on biovolume data for the total phytoplankton at D_1 and D_2; fig. 37 shows the same for the nannophytoplankton fraction at both sampling localities.

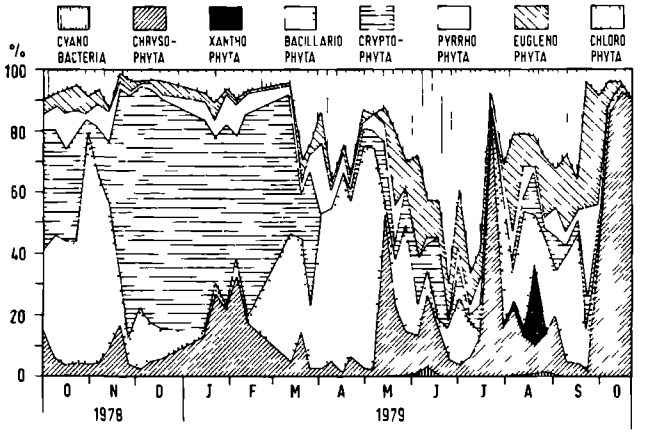


Fig. 32. Percentual contribution to the total biovolume of the various phytoplankton groups. Total phytoplankton of the open water area (D_1) of pond D of the Oude Waal.

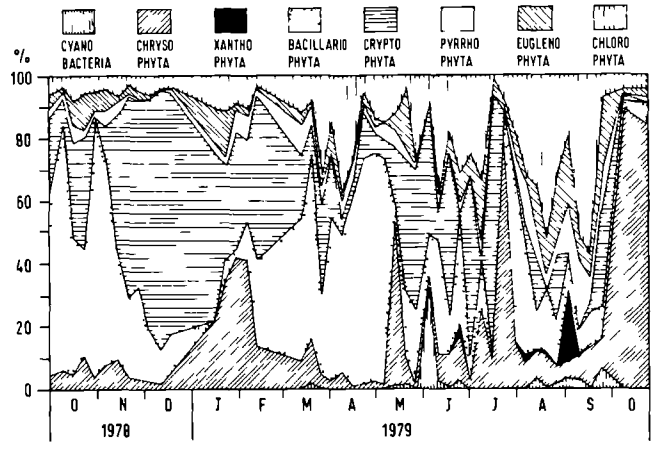


Fig. 33. As fig. 32, Total phytoplankton of the nymphaeid-dominated area (D_2) of pond D of the Oude Waal.

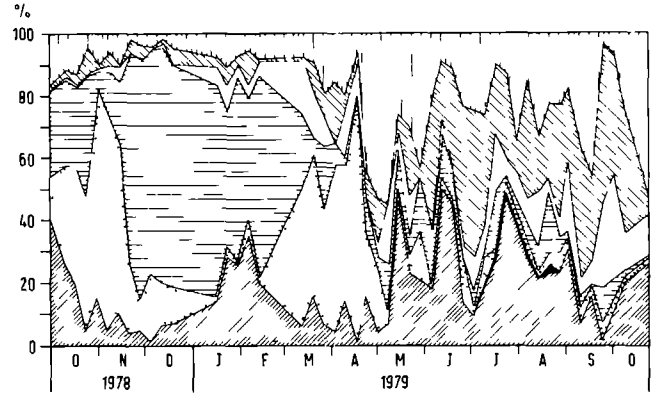


Fig. 34. As fig. 32; Nannophytoplankton of the open water area (D_1) of pond D of the Oude Waal.

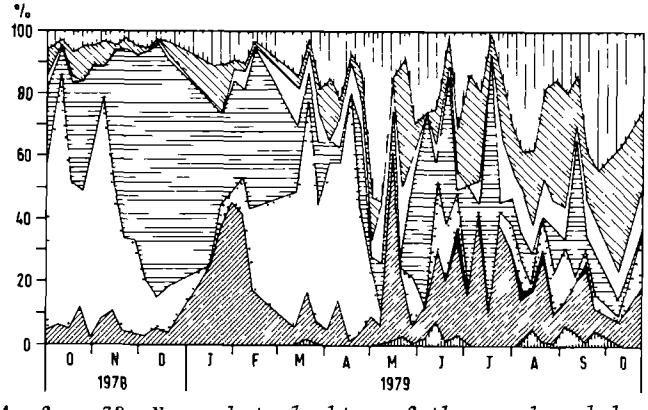


Fig. 35. As fig. 32, Nannophytoplankton of the nymphaeid-dominated area (D_2) of pond D of the Oude Waal.

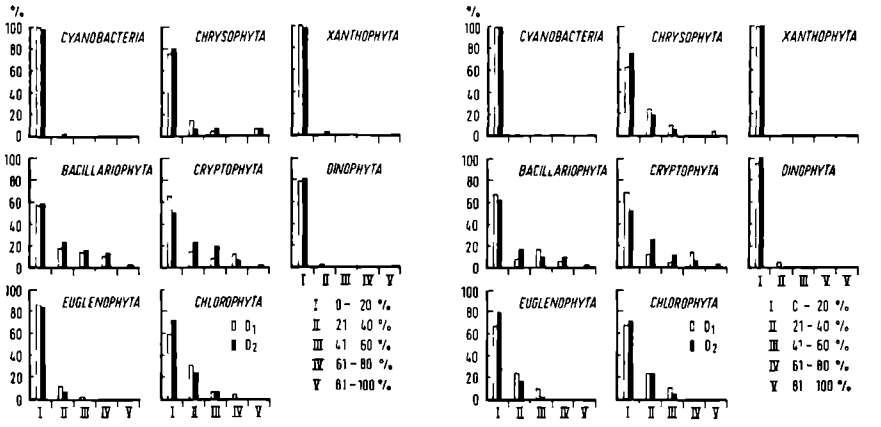


Fig. 36. (left) Frequency distribution of the 8 major algal groups over 5 biovolume classes (frequency with which the algal group was present in each sample). The range of the 5 biovolume classes is indicated in the figure. The data represent the biovolume data of the total phytoplankton in pond D of the Oude Waal. Period: October 1978 to November 1979.
D_1 = open water area; D_2 = nymphaeid-dominated area.

Fig. 37. (right) As fig. 36; Biovolume data of the nannophytoplankton in pond D of the Oude Waal.

Fig. 30 shows that the biovolume of the total phytoplankton at D_1 differs from that at D_2 only in the month of October 1979, during which time the values are much higher at D_2 (nymphaeid-dominated area) than at D_1 (open water area); another difference is found in January, when the phytoplankton biovolume at D_1 was considerably higher than that at D_2. Other differences are insignificant. The course of the biovolume curve shows that there are four periods of biomass increase: October 1978, January/February, July, as well as a gradually increasing biovolume from August to October 1979. Comparing fig. 31 (nannophytoplankton) with fig. 30 (total phytoplankton) we notice that the main difference is the much lower biovolumes at D_1 and D_2 of the nannophytoplankton in July and September/October 1979, both due to the absence of *Synura* spp. in the nannophytoplankton fraction. Everywhere else the curves follow the same course.

A comparison of fig. 32 with fig. 33 reveals only minor differences in the total phytoplankton species composition based on biovolume data. On 9 October 1978 the Diatoms are more important at D_2 than at D_1; fig. 30 shows

that these differences are less important on a quantitative scale. The same is true for the qualitatively more important contribution of the Diatoms to the total phytoplankton species composition on March 19. Greater significance must be attached to the shift in species composition at D_2 (nymphaeid-dominated area), when compared with D_1 (open water area), from Chlorophytes to Cryptophytes during the period May to July, and to the reverse shift from several other groups (Euglenophytes, Diatoms) to Chlorophytes and even to Cyanobacteria. Both these shifts - in June there was also a considerable contribution of Cyanobacteria to the total biovolume of D_2 - point towards an increased nutrient input. In the nannophytoplankton (figs. 34 and 35), Euglenophytes contribute more to the total nannophytoplankton biovolume in June and July than to the total biovolume of the total phytoplankton; this is due to the fact that during this period the Chlorophytes, which usually belong to the size class of the nannophytoplankton, are too large (*Pandorina morum*, *Eudorina elegans*) to be included in this size class.

Figs. 36 and 37 show that among the 8 major algal groups in the total phytoplankton and also in the nannophytoplankton only four groups are frequently present in the samples, constituting more than 20 % of the total biovolume, viz. Diatoms, Cryptophytes, Chlorophytes and Chrysophytes; in the nannophytoplankton Euglenophytes are also frequently present in the samples, constituting more than 20 % of the total biovolume. This again illustrates the quantitative importance of these algal groups (compare also table 12 and table 17).

6.2.2. Dry weight and ash-free dry weight

Dry weight determinations reflect directly upon the organic plus inorganic content of the seston (tripton plus plankton, in other words living and dead material), while ash-free dry weight determinations reflect upon the organic content only. The ash of the seston includes silica compounds, so the question arises whether the weight of a seston sample including many Diatoms, which consist mostly - as far as weight is concerned - of silica, is adequately represented by this biomass measure. In the second place the distinction between living and dead material and between phytoplankton and zooplankton is not drawn. But in terms of energy transfer from the first step to the second step in the food chain it is of no importance whether the organic material available to the second level is dead or alive. It is for this purpose in particular that the ash-free dry weight of the seston has been chosen as an important parameter.

The results of the dry weight determinations and the ash-free dry weight determinations of the total seston samples at D_1 and D_2 are shown in fig. 38 (dry weight) and fig. 39 (ash-free dry weight); the dry weight of the 'nannoseston' at D_1 and D_2 is shown in fig. 40 and the ash-free dry weight of the nannoseston in fig. 41.

There are only slight differences between the two sampling localities D_1 and D_2, both concerning the total seston and the nannoseston fraction of the samples. These differences are most obvious in the period from May to October 1979, when the ash-free dry weight - but also the dry weight - at D_2 (nymphaeid-dominated area) is not only in most cases higher than at D_1 (open water area), but also shows a much more conspicuous fluctuation pattern. It is also clear from the figures that the ash-free dry weight shows a more gradual course than the dry weight. Three periods of (ash-free) dry weight seston peaks could be clearly distinguished: October/November 1978, March/April and June through October 1979.

On the average, the ash-free dry weight of the nannoseston both at D_1 and D_2 was 77 % of the total seston ash-free dry weight; the dry weight of the nannoseston at D_1 was 83 % of the total seston dry weight, at D_2 this was 77 %.

6.2.3. Chlorophyll-a

Unlike the dry weight and the ash-free dry weight, the chlorophyll-a content of a seston sample reflects directly upon the algae. Although some groups of algae posses other pigments than chlorophyll-a as their main photosynthetically active pigments (Round, 1973 Hallegraeff, 1976; van den Hoek, 1978), in phytoplankton research covering a mixed community of many algal species from very different taxonomical groups estimation of the chlorophyll-a content is preferred as a parameter (Hallegraeff, 1976). Chlorophyll-a is a major pigment in all algal groups; the only other pigment also present in all algal groups is β-carotene, but this is undetectable in groups of Cryptophytes (van den Hoek, 1978). For this reason many workers have proposed methods to quantify the chlorophyll-a content in samples of mixed algal species composition (Richards & Thompson, 1952; Lorenzen, 1967; Moss, 1967; Marker, 1972; Nusch & Palme, 1975; Shoaf & Lium, 1976, 1977), while some have proposed methods to quantify the carotenoids in algae as well (Jeffrey, 1961). The chlorophyll-a content of many algae may fluctuate with the physiological state of the algae (Moed &

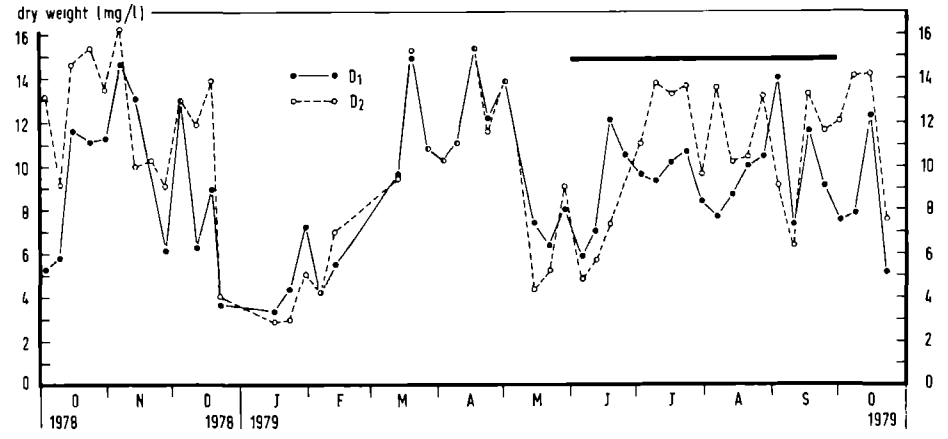


Fig. 38. The dry weight of the total seston as a function of time in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

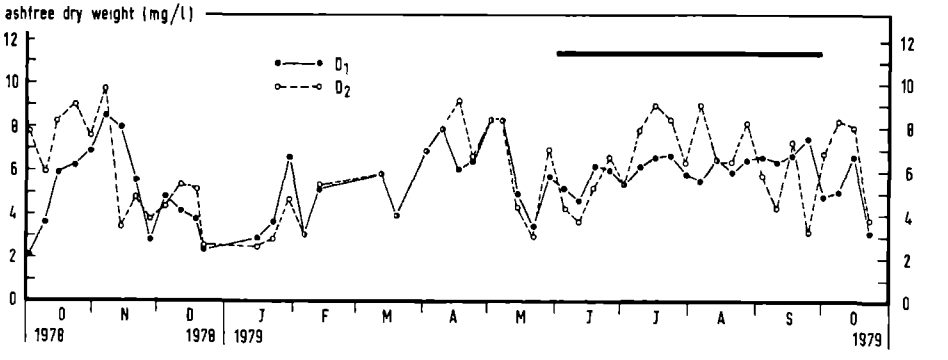


Fig. 39. The ash-free dry weight of the total seston as a function of time in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

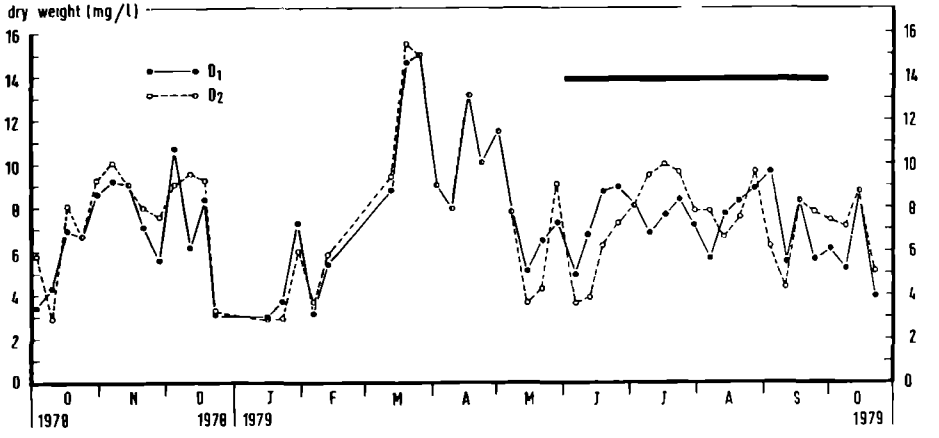


Fig. 40. The dry weight of the nannoseston as a function of time in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

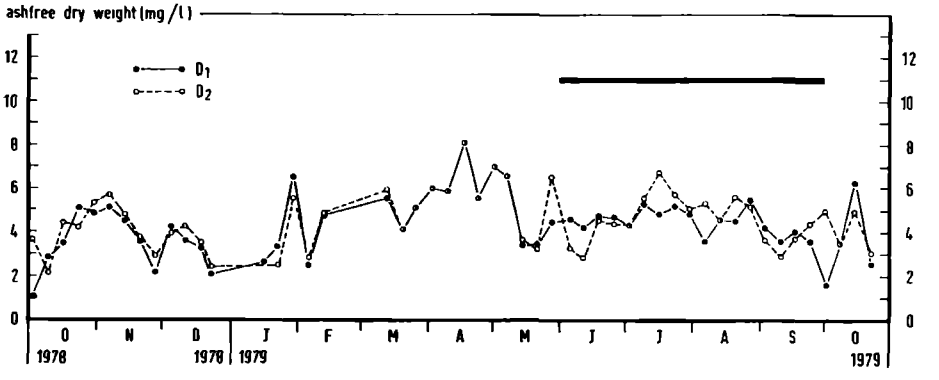


Fig. 41. The ash-free dry weight of the nannoseston as a function of time in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

Hallegraeff, 1978). In fact this is the reason why chlorophyll-a is often used as a measure for the photosynthetically active phytoplankton biomass.

The chlorophyll-a estimation could be interfered with by the presence of chlorophyll-a degradation products (phaeopigments). These degradation products interfere particularly with the results if these are based upon measurements of absorbance at the chlorophyll-a maximum at 665 nm, since the degradation products of chlorophyll-a also have a maximum absorbance at 665 nm. The formula used by Lorenzen (1967) corrects for these interferences.

Due to fluctuations in the chlorophyll-a content of phytoplankton algae a 10 % standard deviation from the mean values for replicate samples is not unusual (Roijackers, 1981a).

The chlorophyll-a content of the total phytoplankton at D_1 and D_2 is shown in fig. 42; the nannophytoplankton chlorophyll-a content is shown in fig. 43.

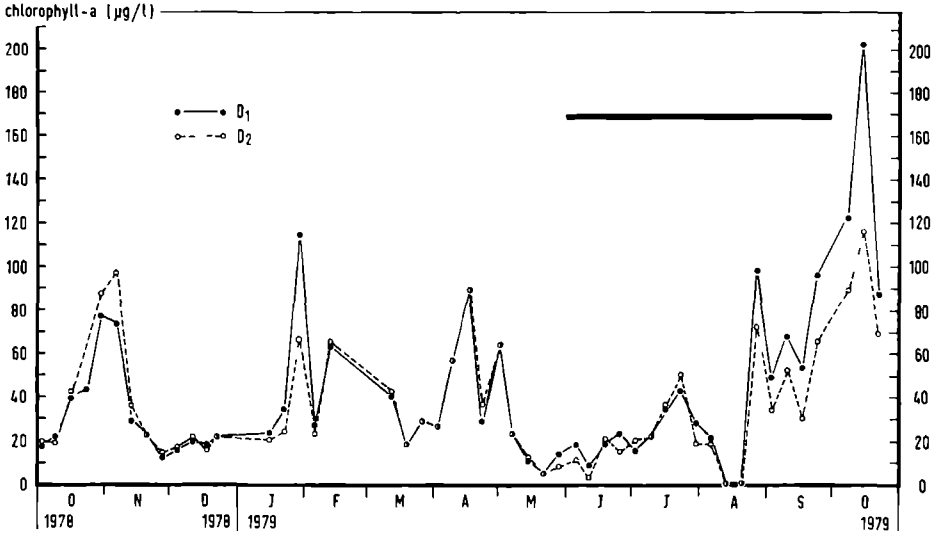


Fig. 42. The chlorophyll-a content of the total phytoplankton as a function of time in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

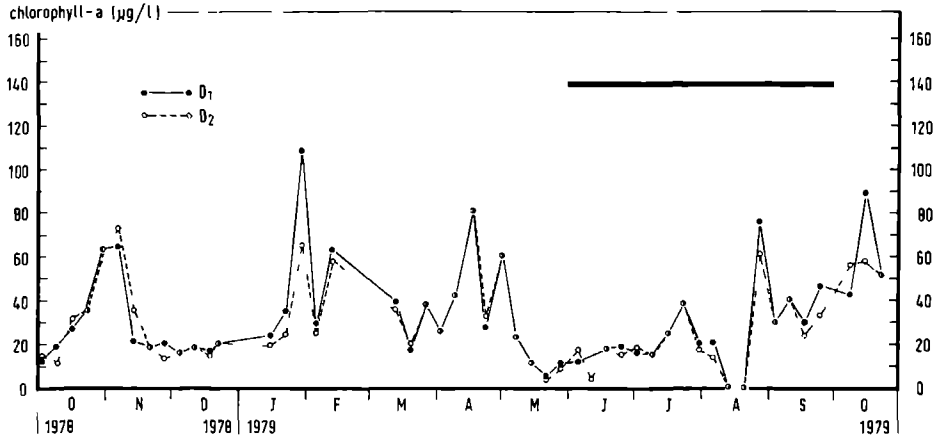


Fig. 43. The chlorophyll-a content of the nannophytoplankton as a function of time in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

The chlorophyll-a content of the total phytoplankton shows a number of peaks: October 1978, January, February, April and August to October 1979. This last increase is more pronounced at D_1 than at D_2. The course of the chlorophyll-a curve of the nannophytoplankton is about the same as that of the total phytoplankton. The differences in chlorophyll-a content between D_1 and D_2 are much smaller in the nannophytoplankton than in the total phytoplankton and only occasionally are they significant (29 January and 15 October 1979).

On average the chlorophyll-a content of the nannophytoplankton is 84 % of that of the total phytoplankton, both at D_1 and D_2.

6.3. DISCUSSION

For the purpose of characterizing the phytoplankton community structure on the basis of its species composition the probability of encounter (Dresscher, 1964) is a useful aid. In tables 9, 10, 13, 14, 15 and 16 and in appendices IIa and b these values are presented for all taxa (column a: total investigation period; column b: period of maximum development of the nymphaeids; column c: period of absence of the above-ground nymphaeid biomass). The probability of encounter is in fact a measure of the frequency of the taxa and it will be used as such in the following text. If a taxon is present in 1 - 20 % of the samples the frequency class is 1; if a taxon is

Table 19. Taxa at sampling locality D_1 (open water area) of pond D of the Oude Waal with frequency classes 5 (first column left), 4 (second column left) and 3 (right column).
5 = present in 81 - 100 % of the samples; 4 = present in 61 - 80 % of the samples; 3 = present in 41 - 60 % of the samples.

Chrysococcus spp.		Kephyrion rubri-claustri
Synura uvella		Stenokalyx monilifera
Stephanodiscus astrea var. minutula		Mallomonas tonsurata
Peridinium spp.		Mallomonas akrokomos
Trachelomonas hispida		Synura petersenii f. praefracta
Trachelomonas volvocina		Synura glabra
Chlamydomonas spp.		Synura curtispina
Ankistrodesmus falcatus		Chromophysomonas trioralis
Scenedesmus quadricauda		Paraphysomonas imperforata
		Paraphysomonas butcheri
		Hymenomonas roseola
		Goniochloris mutica
		Aulacosira italica
		Stephanodiscus astrea
		Diatoma elongatum
		Fragilaria capucina
		Synedra acus
		Synedra ulna
		Navicula radiosa
		Nitzschia acicularis
		Nitzschia palea
Dinobryon sociale		Cryptomonas spp.
Dinobryon divergens		Gymnodinium spp.
Mallomonas acaroides		Eudorina elegans
Mallomonas monograptus		Dictyosphaerium pulchellum
Synura petersenii		Oocystis marsonii
Paraphysomonas vestita		Kirchneriella obesa
Bicocoeca planktonica		Coelastrum microporum
Cyclotella meneghiniana		Tetrastrum staurogeniaeforme
Asterionella formosa		Crucigenia quadrata
Euglena spp.		Crucigenia tetrapedia
Pandorina morum		Scenedesmus bicaudatus
Lagerheimia genevensis		Scenedesmus dimorphus
Monoraphidium contortum		Scenedesmus granulatus
		Scenedesmus tenuispina
		Cosmarium spp.

Table 20. Taxa at sampling locality D_2 (nymphaeid-dominated area) of pond D of the Oude Waal with frequency classes 5 (first column left), 4 (second column left) and 3 (right column).
5 = present in 81 - 100 % of the samples; 4 = present in 61 - 80 % of the samples; 3 = present in 41 - 60 % of the samples.

Chrysococcus spp.		Kephyrion rubri-claustri
Synura uvella		Stenokalyx monilifera
Stephanodiscus astrea var. minutula		Dinobryon sociale
Trachelomonas hispida		Mallomonas tonsurata
Monoraphidium contortum		Mallomonas akrokomos
Chlamydomonas spp.		Chromophysomonas trioralis
		Hymenomonas roseola
		Goniochloris mutica
		Aulacosira italica
		Cyclotella pseudostelligera
		Stephanodiscus astrea
		Diatoma elongatum
		Fragilaria capucina
		Synedra tabulata
		Synedra ulna
		Eunotia lunaris
		Navicula hungarica
		Navicula radiosa
		Navicula rhynchocephala
		Amphora ovalis
		Nitzschia acicularis
		Nitzschia palea
		Cryptomonas spp.
		Gymnodinium spp.
		Euglena polymorpha
		Trachelomonas volvocinopsis
Dinobryon divergens		Eudorina elegans
Mallomonas acaroides		Dictyosphaerium pulchellum
Mallomonas monograptus		Lagerheimia genevensis
Synura petersenii		Oocystis marsonii
Paraphysomonas vestita		Kirchneriella obesa
Bicocoeca planktonica		Coelastrum microporum
Cyclotella meneghiniana		Tetrastrum staurogeniaeforme
Asterionella formosa		Crucigenia quadrata
Navicula radiosa		Crucigenia tetrapedia
Peridinium spp.		Scenedesmus bicaudatus
Trachelomonas volvocina		Scenedesmus dimorphus
Pandorina morum		Scenedesmus granulatus
Ankistrodesmus falcatus		Scenedesmus tenuispina
Scenedesmus quadricauda		Cosmarium spp.

present in 21 - 40 % of the samples the frequency class is 2, etc.

In tables 19 and 20 the taxa have been arranged in three columns according to their frequency class (over the entire investigation period); for taxa in the first column (left) the frequency class is 5; for those in the second column (left) the frequency class is 4 and for those in the third column (right) the frequency class is 3. Table 19 gives the taxa for D_1 (open water area), table 20 those for D_2 (nymphaeid-dominated area).

On the basis of these two tables one might define the typical combination of phytoplankton taxa occurring in pond D of the Oude Waal. This combination consists of those taxa present throughout the year in that pond (frequency class 5). The following combination is characteristic for the pond:

Chrysococcus spp. (*C. biporus/C. minutus/C. porifer/ C. rufescens*)
Synura uvella
Stephanodiscus astrea var. *minutula*
Chlamydomonas spp.

This basic combination must be supplemented with the following taxa for D_1:

Peridinium spp.
Trachelomonas volvocina
Ankistrodesmus falcatus
Scenedesmus quadricauda

These taxa are also present at D_2, in the lower frequency class 4 (in 61 to 80 % of the samples, or in 61 to 80 % of the year.
For sampling locality D_2 the basic combination must be supplemented with:

Monoraphidium contortum

and this species is also present in D_1, in the lower frequency class 4.

On the basis of these results there is no clear difference between the two sampling localities in pond D, which is not surprising, since the most prominent difference between the two sampling localities - the aboveground nymphaeid parts - exists only for a part of the year. Differences - if any - should be looked for during the nymphaeid development period.

The following taxa could be added to the basic combination in order to extend it to include those taxa which characterize the phytoplankton communities during a considerable part of the year (at least at one of the sampling localities in 61 to 80 % of the samples). However these taxa do not necessarily occur at the same moment.

Dinobryon divergens
(Dinobryon sociale)
Mallomonas acaroides

Mallomonas monograplus
Synura petersenii
Paraphysomonas vestita
Bicocoeca planktonica
Cyclotella meneghiniana
Asterionella formosa
(Navicula radiosa)
Pandorina morum
(Lagerheimia genevensis)

The species between brackets have a frequency class of 3 at either D_1 or D_2; the other species in the list have a frequency class of 4 at both sampling localities.

Here a clear difference between the two sampling localities is found. *Euglena*-species were often (in 61 - 80 % of the samples) found at sampling locality D_1 (open water area), whereas the group of unidentified *Euglena*-species was only present in 1 - 20 % of the samples from D_2 (nymphaeid-dominated area).

With regard to the presence of the taxa as indicated in tables 9, 10, 13, 14, 15 and 16 the correlation between the occurrence of nymphaeids and the presence or abundance of the phytoplankton taxa could be analysed by comparing the frequency during the period of absence of the nymphaeids (December 1978 to April 1979) and that during the presence of the nymphaeids (October to November 1978 and May to October 1979). Where the frequency classes in these two periods differ more than 2 units, the differences are considered to be significant. If in these cases results for sampling locality D_1 (open water area) are the same as those for sampling locality D_2 (nymphaeid-dominated area) the differences can be attributed to the seasonal development of the phytoplankton. But if the differences are not the same for D_1 and D_2, a connection with the aboveground biomass of the nymphaeids is highly probable.

The following four categories of taxa can be distinguished, based on the above-mentioned analyses.

a. taxa mainly present during the period of nymphaeid development, but whose presence is not influenced by the nymphaeids:

Stenokalyx inconstans
Dinobryon sociale
Dinobryon divergens
Mallomonas acaroides
Mallomonas tonsurata
Mallomonas caudata
Synura curtispina
Chromophysomonas trioralis
Paraphysomonas diademifera
Hymenomonas roseola

the entire group of Xanthophyta, but particularly: *Goniochloris mutica*
Aulacosira granulata
Cyclotella meneghiniana
Cyclotella pseudostelligera
Diatoma elongatum
Fragilaria capucina
Synedra acus
Cocconeis placentula
Navicula cryptocephala
Nitzschia acicularis
Nitzschia palea
Trachelomonas planktonica
Pteromonas angulosa
Pediastrum duplex
Kirchneriella obesa
Scenedesmus quadricauda

b. taxa mainly present during the period in which the nymphaeids are in dormancy, but whose absence during the period of nymphaeid development is not influenced by the nymphaeids:

Pseudokephyrion poculum
Mallomonas akrokomos
Synura glabra
Stephanodiscus astrea
Asterionella formosa
Navicula viridula
Phacus pyrum
Trachelomonas volvocinopsis
Eudorina elegans
Oocystis marsonii
cf. *Monoraphidium arcuatum*
Monoraphidium minimum
Quadrigula lacustris
Tetrastrum glabrum
Tetrastrum staurogeniaeforme
Scenedesmus granulata

c. taxa present during the period of nymphaeid development and particularly in the nymphaeid-dominated area of the pond:

Stenokalyx monilifera
Bicocoeca planktonica
Euglena polymorpha
Cosmarium spp.

d. taxa present during the period of nymphaeid development, and mainly present in the open water area of the pond:

Euglena spp.

These lists show that the presence and/or abundance of the phytoplankton taxa in pond D is not determined to any important extent by the presence or absence of the nymphaeids. In some situations both the seasonality of the taxa and the presence or absence of the nymphaeids influence the presence or absence of the phytoplankton taxa.

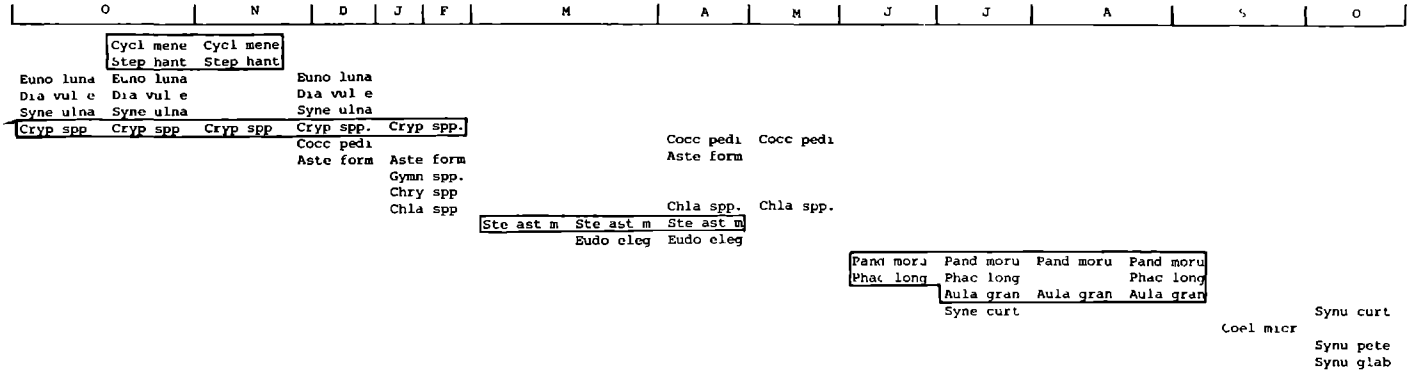
An association is a recurrent group of co-occurring species (Legendre & Legendre, 1978). An association can consist of a wide variety of taxa, all of which have their own characteristic growth rates and nutrient requirements (Reynolds, 1982), so that a given association of phytoplankton organisms reflects the structure of the phytoplankton community at any given moment. But at any such moment the association represents only one particular stage of a continuously changing phytoplankton community. Sometimes these changes are slow and in that case the phytoplankton species composition may be stable for a long period of time; but sometimes rapid environmental changes take place and the changes in the phytoplankton species composition may then become more rapid. In summary, one could expect to register phytoplankton associations persisting for periods lasting from one to several weeks, depending on the environmental circumstances.

The phytoplankton associations at the sampling localities in pond D must consist of the taxa listed in tables 9, 13 and 15 for the open water area (D_1) and those in tables 10, 14 and 16 for the nymphaeid-dominated area (D_2). These associations will be characterized by the dominant taxa distinguished through the biovolume determinations. Table 21 illustrates the developments in phytoplankton associations at D_1 as reflected by their dominants. The situation for D_2 is essentially the same.

Table 21 shows that particularly in the colder months the dominants remain the same for a long period of time, and it is obvious that at the actual moments when shifts in dominance occur some species are able to develop large populations. Sometimes these persist for several weeks, but in most cases just for a few days.

Calling to mind the theories of r-selected (opportunistic) species and K-selected (equilibrium) species, originally devised by MacArthur & Wilson (1967), further developed by Hairston et al. (1970), Pianka (1970, 1972) and Margalef (1977), and applied to phytoplankton ecology especially by Kilham & Kilham (1980), Sommer (1981) and Reynolds (1982, 1984), the 15 associations listed in table 21 may be divided into 5 groups of K-selected type taxa and 3 to 4 groups of r-selected type taxa. The groups of K-selected type taxa have been boxed in the table. The r-selected type taxa are *Gymnodinium* spp., *Chrysococcus* spp., *Chlamydomonas* spp., *Coelastrum*

Table 21. The succession of dominant phytoplankton taxa at sampling locality D_1 (open water area) in pond D of the Oude Waal.
The data are based on biovolume determinations. Generic and species names have been abbreviated. The blocks indicate K-selected type taxa.



microporum, *Synura curtispina*, *Synura petersenii* and *Synura glabra* and, less clearly *Asterionella formosa* and *Cocconeis pediculus* (cf. Reynolds, 1982). It is most likely that *Cryptomonas* spp. also belongs to the r-selected type taxa. These taxa have the possibility to grow rapidly under conditions which are favourable to them during a relatively short period. In the long run, however, they will be replaced by K-selected type taxa, as one or more factors (nutrients, irradiance, temperature) become limiting. K-selected species are characterized by their ability to minimize the possibilities for competition by other algae, for instance through making essential nutrients unavailable to potentially competing algae by increasing nutrient storage for non-limiting nutrients (Tilman & Kilham, 1976; Kilham et al., 1976; Rhee, 1978) or by specific chelation of micro-nutrients (Murphy et al., 1976). K-selected species grow slowly and have a low productivity level, but they are highly efficient in utilizing the factors they need for their development (Kilham & Kilham, 1980). K-selected type taxa in table 21 are *Cyclotella meneghiniana*, *Stephanodiscus hantzschii*, *Stephanodiscus astrea* var. *minutula* and *Aulacosira granulata*, all centric Diatoms.

Fig. 43 shows that the general phytoplankton biomass development pattern in pond D of the Oude Waal corresponds closely to the biomass fluctuation patterns of shallow, productive lakes (Reynolds, 1984). It is to be expected that this dimictic sequence, which is also known - in a more complex cycle - for other productive temperate lakes (Hutchinson, 1967), is typical for the Oude Waal (see also fig. 22, pond F of the Oude Waal). Hence the basic phytoplankton biomass development pattern will be about the same every year, although the species which cause the biomass peaks can differ from year to year (although they all will belong to the r-selected type taxa, the fast growing ones). In pond D of the Oude Waal many such taxa have the potential to develop, depending on minute differences in growth-determining factors (irradiance, temperature, nutrients, etc.). However, K-selected type taxa will always be present as well, allthough in small quantities.

The use of the three different methods to determine the phytoplankton biomass enables us to look at the phytoplankton community from three different angles of approach (Hallegraeff, 1976). If we compare the dry weight and the ash-free dry weight of the seston at both sampling localities, there are two periods in which the difference between the two measures (i.e. the ash content of the seston) is small. In these two periods there was little

disturbance of the water column, since in January the pond was entirely covered by a 10 - 15 cm thick layer of ice and in May, at least at the sampling dates, there was no wind action. In the periods in between either turbulence, caused by the wind, or input of allochtonous material resulted in a higher seston content of the water column, as reflected by the higher dry weight and greater discrepancies between dry weight and ash-free dry weight. Both factors (resuspension of settled material and sedimentation of allochtonous material) contribute significantly to the total seston dry weight. Essentially, the basic - high - ash-free dry weight content of the seston in pond D of the Oude Waal does not allow the distinction of minor phytoplankton biomass increases, as the phytoplankton component of the seston is very small (Vollenweider, 1974; Wetzel, 1975; Hallegraeff, 1976; the present study).

In comparing the ash-free dry weight of the seston at D_1 with the ash-free dry weight at D_2 it is found that marked differences occur during the period July to October 1979. The higher values at D_2 (nymphaeid-dominated area) are clearly the result of the larger amount of organic material stemming from the continuously decaying nymphaeids during that period. The fluctuation pattern in the ash-free dry weight content at D_2 also points to an influence of wind and wave action upon the resuspension of settled (macrophyte and periphyton) material.

A better picture of the phytoplankton biomass is given by the chlorophyll-a content of the phytoplankton. The chlorophyll-a content of an algal cell may vary widely under the influence of various factors such as cell age, nutrient availability, irradiance, temperature etc. (Strickland, 1960; Steele & Baird, 1961, 1962, 1965). Furthermore the chlorophyll-a content of algae only reflects upon a very small part of the algal biomass. Hence, not every increase in the chlorophyll-a content of phytoplankton is an actual biomass increase; it merely provides information about the potential biomass increase, since a higher chlorophyll-a content may result in a higher production level. The chlorophyll-a fluctuation pattern reveals several peaks for both sampling localities. Most of these peaks could be correlated with phytoplankton blooms of several species, as revealed by the biovolume fluctuation pattern. Obvious biomass increases are attributable to *Cyclotella meneghiniana* and *Stephanodiscus hantzschii* (October - November 1978), to *Chrysococcus* spp. (January and February) and *Asterionella formosa* (February), to *Synura curtispina* (July) and to *Synura petersenii*, together with *Synura*

glabra and *Synura curtispina* (October 1979). The chlorophyll-a increase in March, however, is not found back in the biovolume at that moment. This is due to the minute dimensions of the algae in question (*Stephanodiscus astrea* var. *minutula*). A second period of chlorophyll-a increase in the phytoplankton which is not corroborated by the biovolume data starts at the end of August and persists during September. This increase is attributable to the growth and decline of populations of *Pandorina morum*. In comparing the chlorophyll-a content of the phytoplankton at D_1 (open water area) with that of the phytoplankton at D_2 (nymphaeid-dominated area) a higher content is found at D_1 in the period August to October 1979, which is due to the lower irradiance levels at D_2, in combination with the phytoplankton species composition at that moment (which is the same for D_1 and D_2!).

Laboratory experiments have shown that in algae the cellular chlorophyll-a contents decrease if the cells are cultured at higher irradiance intensities (Myers, 1946a, 1946b; Brown & Richardson, 1968, Sheridan, 1972a, 1972b). The irradiance level has been described as an important factor in the regulation of phytoplankton chlorophyll-a content per cell unit (Harris, 1978). Below irradiance levels of 100 $\mu E/m^2$.sec there is a marked increase in cellular chlorophyll-a concentrations, but also in photosynthetic membrane content and accessory pigment content. In table 22 the period May to October 1979 (maximum development period of the nymphaeids) has been divided into the two periods previously mentioned (May - August and August - October), as a direct consequence of the shape of the chlorophyll-a curve during that period of nymphaeid development. In the table the number of sampling dates at which the irradiance level (under water at 15 cm) was a) below 100 $\mu E/m^2$.sec, b) between 100 and 200 $\mu E/m^2$.sec and c) above 200 $\mu E/m^2$.sec have been indicated as percentages of the total number of sampling dates during that period (May to October 1979). The value 100 $\mu E/m^2$.sec represents the limit below which adaptation by phytoplankton through the increase of chlorophyll-a per cell unit may occur; the value 200 $\mu E/m^2$.sec represents the limit above which photoinhibition may occur (Harris, 1978).

As can be seen from this table the irradiance level at D_1 (open water area) is well above the 100 $\mu E/m^2$.sec mark during the entire period and even at most dates above the 200 $\mu E/m^2$.sec mark. It may well be that the phytoplankton at D_2 (nymphaeid-dominated area) is much better adapted to low irradiance levels during the period May to Augustus than to those during the period August to October 1979.

Table 22. Frequency of sampling dates (as percentages of the total number in the period May to October) at which the irradiance level was as indicated.
D_1: open water area ; D_2: nymphaeid-dominated area of pond D of the Oude Waal.
Values in $\mu E/m^2.sec$ (under water at 15 cm).

		<100	100-200	>200
D_1	May - August	14 %	29 %	57 %
	August - October	22 %	22 %	56 %
D_2	May - August	64 %	7 %	29 %
	August - October	44 %	44 %	12 %

An explanation of the lower chlorophyll-a content of the phytoplankton at D_2 (nymphaeid-dominated area), as compared to D_1 (open water area), in the period August to September, is thus certainly not to be found in the irradiance level alone. It is most probable that the dominance of *Pandorina morum* during that period plays an important role. Presumably this species needs higher irradiance levels to increase its chlorophyll-a content per cell unit than do other taxa, which are dominant in the period before and after the dominance of *Pandorina morum*. The irradiance level at D_2 during the period August to October, although already higher than that during the period May to August, is still too low to allow *Pandorina morum* to increase its chlorophyll-a content. In pond F the same was found for again *Pandorina morum*, but particularly *Pteromonas angulosa*, both dominant at the period July to September 1977. In that period again the chlorophyll-a content of the phytoplankton at the nymphaeid-dominated area (F_2) was significantly lower than that at the open water area (F_1).

Seasonal changes in biomass, whether measured as chlorophyll-a, dry weight, ash-free dry weight or biovolume, are the same for the nannophytoplankton and the total phytoplankton. The biomass of the nannophytoplankton is sometimes considerably less than the biomass of the total phytoplankton, but on average it constitutes 60 to 80 % of the total phytoplankton biomass, depending on the sampling locality and the method for measuring biomass used. Table 23 summarizes the percentual contributions of the nannophytoplankton to the total phytoplankton biomass as determined by the various methods. It is striking that - considering the entire investigation period - all biomass estimates result in the same ratio, particularly at D_2 (nymphaeid-dominated area).

Table 23. Percentual contributions of the nannophytoplankton to the total phytoplankton biomass at pond D of the Oude Waal. Values for D_1 (open water area) and D_2 (nymphaeid-dominated area), for the total investigation period and for the period May to October 1979 (maximum development of the nymphaeids).

	total investigation period		May to October 1979	
	D_1	D_2	D_1	D_2
chlorophyll-a	64 %	73 %	83 %	96 %
dry weight	81 %	73 %	80 %	63 %
ash-free dry weight	75 %	74 %	75 %	68 %
biovolume	62 %	63 %	45 %	47 %

7. PRIMARY PRODUCTIVITY OF THE PHYTOPLANKTON IN POND D

7.1. INTRODUCTION

Phytoplankton primary productivity is primarily regulated by photosynthetically active biomass (chlorophyll-a), irradiance (PhAR) and temperature. The chlorophyll-a content is dependent among other things on the phytoplankton species composition and the physiological state of the algae (see Chapter 6, Section 6.2.3.). Many studies have focussed on the relation between irradiance and productivity (Talling, 1971; Hillbricht-Ilkowska et al., 1972; Jewson, 1975; Hickman, 1971, 1976; Hickman & Jenkerson, 1978). The irradiance level varies with depth (Goldman, 1960, 1968; Hickman, 1971, 1976; Hickman & Jenkerson, 1978), with the time of day (Jones, 1978; Gargas et al., 1979; Tilzer & Horne, 1979), with the season (Dubinsky & Berman, 1979), with the amount of suspended particles, whether living or non-living (Tyler & Smith, 1970; Parsons & Takahashi, 1973; Bannister, 1974; Tyler, 1975), etc.. Individually or in combination, all these factors may affect the primary productivity of the phytoplankton populations.

It is obvious that in comparing the open water area with the nymphaeid-dominated area of the pond, the phytoplankton primary productivity will be influenced by the difference between the irradiance levels in the open water area and those in the water column under the floating leaves of the nymphaeids (see fig. 19).

7.2. SEASONAL FLUCTUATIONS IN PRODUCTIVITY AND RELATED VARIABLES.

7.2.1. Productivity

Phytoplankton gross primary productivity in the open water area (D_1) and in the nymphaeid-dominated area (D_2) have been plotted against time in figs. 44 and 45. Table 24 summarizes the mean, maximum and minimum values for productivity during the total period of investigation, as well as separate values for the period of June to September, during which the degree of coverage by floating leaves of nymphaeids reached a peak.

In comparing the productivity fluctuation pattern with the fluctuations in the phytoplankton biovolume (figs. 30 and 31) it is obvious

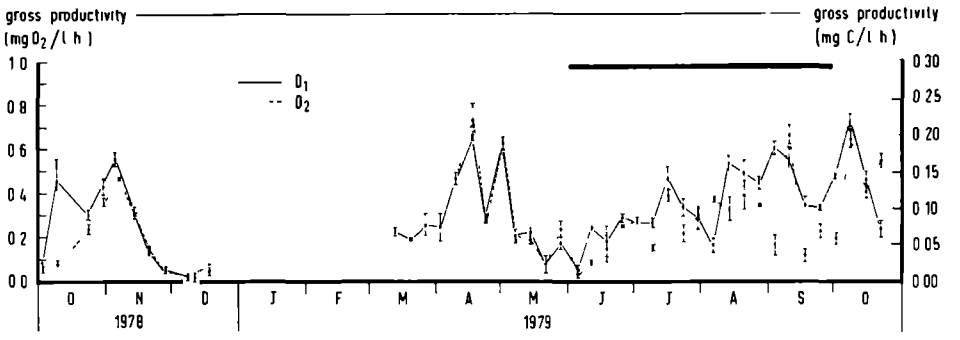


Fig. 44. Primary productivity of the total phytoplankton in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

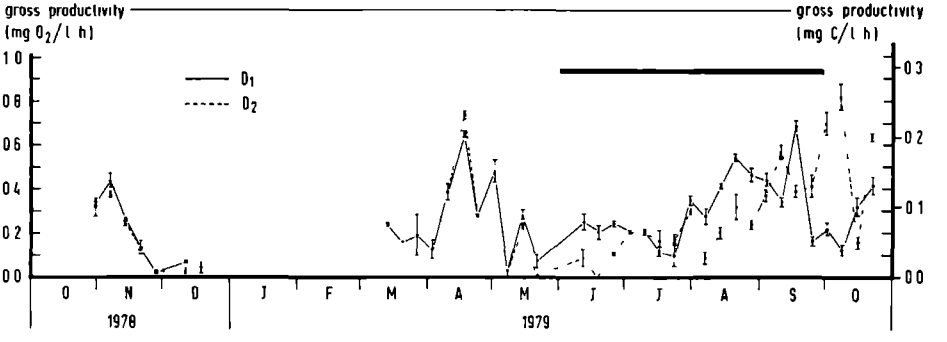


Fig. 45. Primary productivity of the nannophytoplankton in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

Table 24. Mean, maximum and minimum values for the chlorophyll-a content, productivity, pigment efficiency, renewal rate, productivity efficiency and quantum efficiency of the phytoplankton in pond D of the Oude Waal. D_1 = open water area; D_2 = nymphaeid-dominated area.

	chlorophyll-a (µg/l)		productivity mg O_2/l.h)		pigm. eff. (mg O_2/ µg chlor.-a.h)		renewal rate (day^{-1})		prod.eff. mg $O_2.m^2$/ µg chlor.-a.E)		quantum eff. (%)	
Total phytoplankton												
a. total investigation period	D_1	D_2	D_1	D_2	D_1	D_2	D_1	D_2	D_1	D_2	D_1	D_2
mean	42.20	37.43	0.33	0.27	0.009	0.009	0.79	0.65	0.016	0.042	11.2	18.7
maximum	203.04	116.51	0.73	0.73	0.027	0.026	2.68	2.61	0.094	0.268	85.7	106.7
minimum	1.10	1.07	0.04	0.02	0.003	0.001	0.01	0.12	0.000	0.001	0.5	0.3
b. period June to September												
mean	35.83	28.31	0.35	0.26	0.010	0.010	1.07	0.65	0.020	0.086	7.1	29.9
Nannophytoplankton												
a. total investigation period												
mean	32.20	30.72	0.27	0.28	0.009	0.009	0.79	0.90	0.016	0.049	7.8	18.4
maximum	89.04	81.73	0.68	0.81	0.024	0.022	3.09	3.05	0.089	0.330	66.8	106.7
minimum	0.00	0.79	0.00	0.01	0.000	0.000	0.00	0.07	0.000	0.001	0.0	0.1
b. period June to September												
mean	25.87	22.32	0.29	0.25	0.010	0.011	1.19	1.26	0.019	0.101	5.7	26.7

that some biovolume peaks result in productivity increase while others do not. The first productivity increase in October and November 1978 corresponds with a biovolume increase of the centric diatoms *Cyclotella meneghiniana* and *Stephanodiscus hantzschii*. The productivity peak at D_1 in October 1978 is not found back at D_2 and cannot be explained by phytoplankton biovolume differences. After the maximum biomass development of the centric diatoms the productivity level drops rapidly. A second productivity increase is observed in April, both at D_1 and at D_2, but with a smaller biovolume increase, again of a centric diatom (*Stephanodiscus astrea* var. *minutula*). This organism persists for over one month with a fairly constant population and gradually increases its productivity level. The period of May to October is characterized by rather low biovolume of the phytoplankton community, due to a frequent change in species. Still a tendency towards an increase in productivity is observed, culminating in a high productivity level in August and September, which is largely attributable to the centric diatom genera *Aulacosira* and *Melosira*, together with several green algae. Eventually the marked increase in biovolume in October 1979, caused by several *Synura*-species, is also accompanied by a higher productivity level at both sampling localities for this period.

7.2.2. Pigment efficiency and phytoplankton renewal rate.

The pigment efficiency at D_1 and at D_2 has been plotted against time in figs. 46 and 47. The phytoplankton renewal rate at D_1 and D_2 is shown in figs. 48 and 49 for the total phytoplankton and the nannophytoplankton fraction respectively. In table 24 the mean, maximum and minimum values have been summarized for the total investigation period and for the period from June to September.

The values of the pigment efficiency are well within the range recorded by Odum (1971) for lakes and oceans (1-10 mg O_2/mg chlor.-a.h = 0.3-3.1 mg C/mg chlor.-a.h). Comparison of figs. 46 and 47 with figs. 44 and 45 shows two differences. In the first place the differences between the productivity levels at D_1 and D_2 are not reflected in differences in the pigment efficiency of the phytoplankton for both sampling localities. The higher productivity level at D_1 is apparently the result of the higher chlorophyll-a content of the phytoplankton at

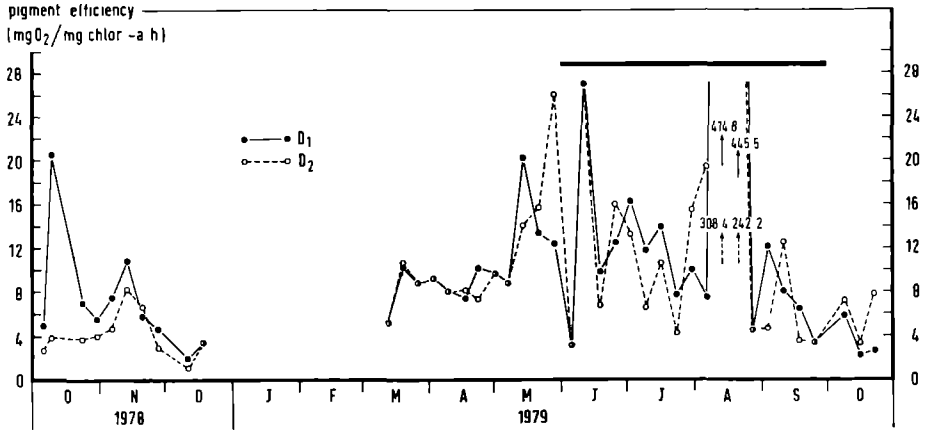


Fig. 46. Pigment efficiency of the total phytoplankton in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

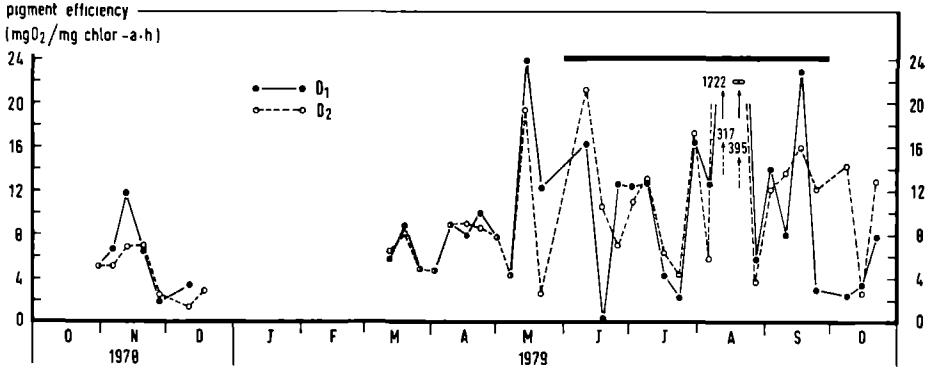


Fig. 47. Pigment efficiency of the nannophytoplankton in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

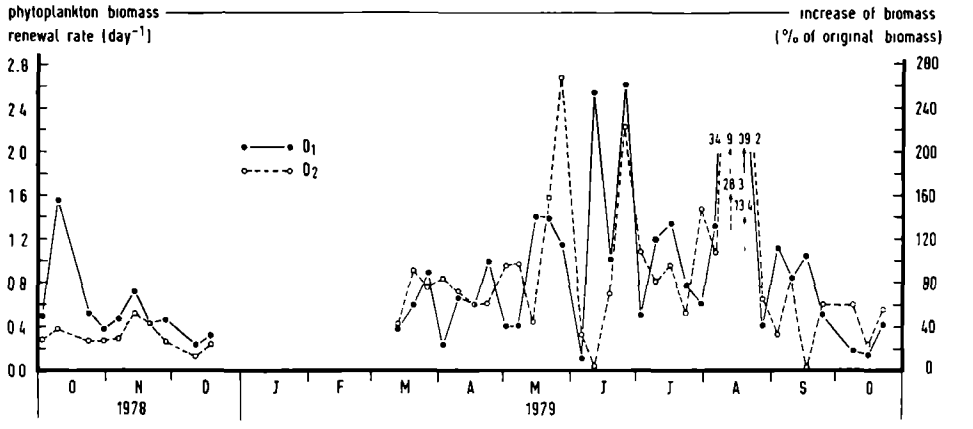


Fig. 48. Renewal rate (turn-over rate; P/B-ratio) of the total phytoplankton in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

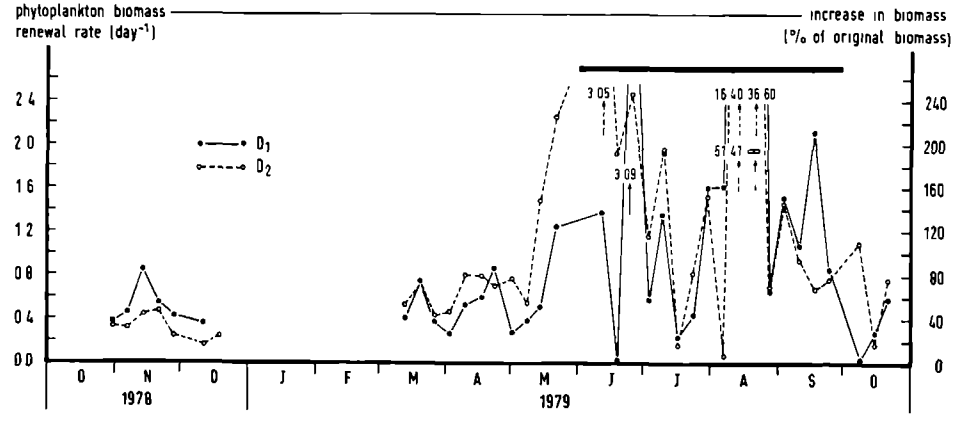


Fig. 49. Renewal rate (turn-over rate; P/B-ratio) of the nannophytoplankton in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

that sampling locality (see also figs. 42 and 43). In the second place the shape of the pigment efficiency curve is quite similar to that of the water temperature curve (see fig. 20). Linear regression (y = ax+b) of chlorophyll-a, productivity, pigment efficiency and renewal rate versus water temperature resulted in the correlation coefficients listed in table 25. Neither the chlorophyll-a content of the phytoplankton nor its productivity are correlated to the water temperature: there is a slight correlation between the pigment efficiency of the phytoplankton and the water temperature, and this correlation is better for the total phytoplankton fraction in the open water area (D_1) and for the nannophytoplankton fraction in the nymphaeid-dominated area (D_2).

Table 25. Correlation coefficients (r^2) of the linear regression (y=ax+b) of the relation between water temperature and the variables indicated in the table.
D_1 = open water area and D_2 = nymphaeid-dominated area at pond D of the Oude Waal.

	Total phytoplankton		Nannophytoplankton	
	D_1	D_2	D_1	D_2
chlorophyll-a	0.02	-0.09	-0.12	-0.20
productivity	-0.05	0.17	0.18	0.10
pigment efficiency	0.48	0.29	0.39	0.48
renewal rate	0.51	0.54	0.51	0.45

The shape of the curves for the total as well as the nannophytoplankton renewal rate (turn-over rate; P/B-ratio) at both sampling localities differs little from the shapes of the phytoplankton pigment efficiency curves as shown in figs. 46 and 47. This is the result of the minor differences between the net productivity and the gross productivity of the phytoplankton in pond D. The correlation between the phytoplankton renewal rate and the water temperature is even better than that between the phytoplankton pigment efficiency and the water temperature, the best correlation is found for the total phytoplankton at the nymphaeid-dominated area of the pond, but the nannophytoplankton at this sampling locality is less clearly correlated to the water temperature.

7.2.3. Productivity efficiency and quantum efficiency.

The phytoplankton gross productivity efficiency at D_1 and D_2 is shown

in figs. 50 and 51 for the total phytoplankton and the nannophytoplankton fraction respectively. The quantum efficiency is shown in fig. 52 for the total phytoplankton at both sampling localities and in fig. 53 for the nannophytoplankton at both sampling localities. Mean, maximum and minimum values for the total investigation period and for the period of June to September are listed in table 24. The gross productivity efficiency values are well within the range of 6.10^{-3} - 120.10^{-3}, peaking between 20.10^{-3} - 60.10^{-3} mg $O_2.m^2/\mu g$ chlor.-a.E, which is in agreement with what has been reported by others (Jørgensen, 1964; Platt & Jassby, 1976; Harris, 1978; Reynolds, 1984). It is obvious that the productivity efficiency at sampling locality D_2 (the nymphaeid-dominated area) is higher than that at D_1 (the open water area), since at D_2 the underwater irradiance levels are lower, due to the shading by the floating leaves of the nymphaeids at that locality during the vegetation period.

The most obvious difference between the two efficiency quotients used here is the fact that in the quantum efficiency the total phytoplankton community is included, whereas in the productivity efficiency the efficiency per biomass (chlorophyll-a) is expressed. As shown in figs. 52 and 53 the quantum efficiency is also higher in the nymphaeid-dominated area than in the open water area for the period of maximum development of the nymphaeids. This is again due to the use of the underwater irradiance in the quotient; to illustrate this, the quantum efficiency for the total phytoplankton at both sampling localities has also been calculated using the above-surface irradiance instead of the underwater irradiance; the quantum efficiencies thus calculated are also given in fig. 52 for the period of maximum difference between D_1 and D_2 (vegetation period); this figure shows the quantum efficiencies for the phytoplankton at both sampling localities to be about the same in that case.

7.3. DISCUSSION

The productivity fluctuation pattern over the year as illustrated in fig. 44 is typical for an eutrophic fresh-water body (Wetzel, 1975). In order to compare the productivity data from the present investigation with those from other studies it is convenient to express all productivity data as mg C per unit volume or per unit area, using the conversion factors mentioned in Chapter 3.

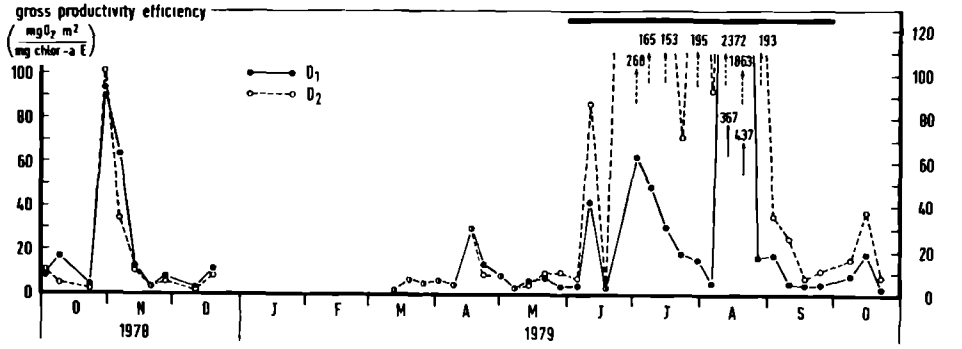


Fig. 50. Gross productivity efficiency of the total phytoplankton in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

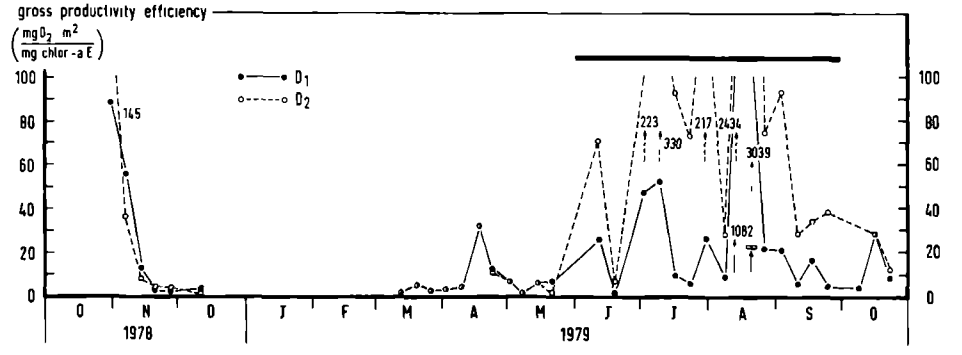


Fig. 51. Gross productivity efficiency of the nannophytoplankton in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

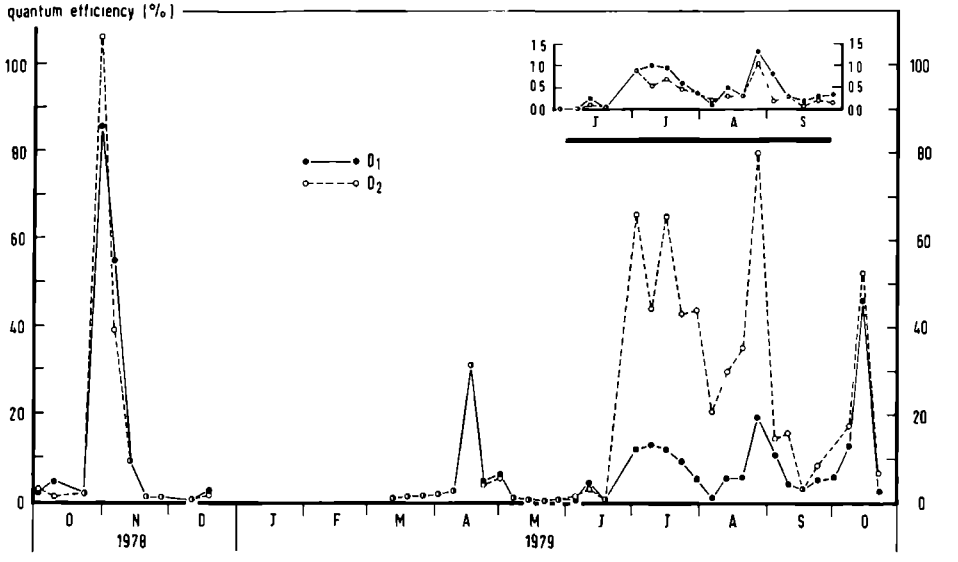


Fig. 52. Quantum efficiency, based on underwater irradiance, of the total phytoplankton in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. Over the period June to September the quantum efficiency, based on incident irradiance, is also shown. D_1 = open water area; D_2 = nymphaeid-dominated area.

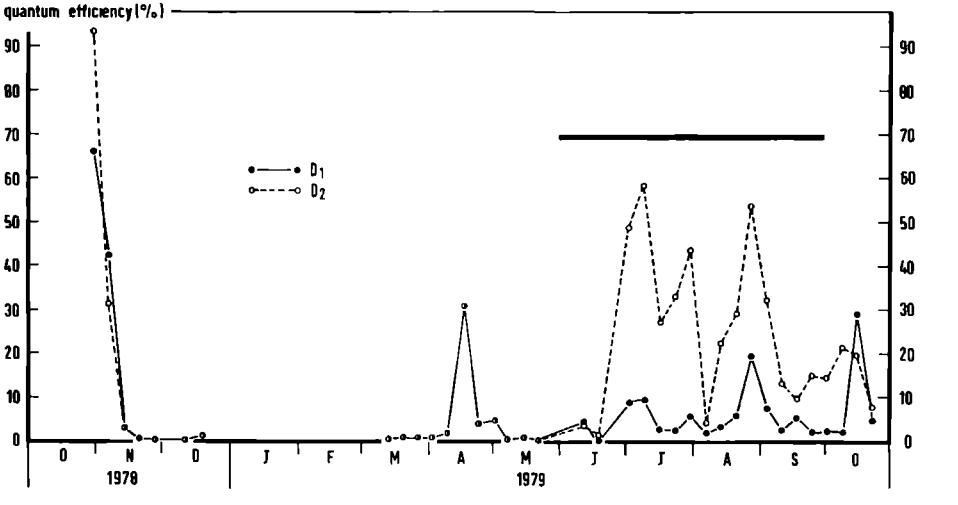


Fig. 53. Quantum efficiency, based on underwater irradiance, of the nannophytoplankton in pond D of the Oude Waal. The period of maximum development of the floating leaves of the nymphaeids is indicated. D_1 = open water area; D_2 = nymphaeid-dominated area.

The mean daily production of the total phytoplankton in the open water area (D_1) is 1.7 g C/m^2 for the entire year and 2.4 g C/m^2 during the vegetation period; in the nymphaeid-dominated area (D_2) these values are 1.4 g C/m^2 for the entire year and 1.8 g C/m^2 for the vegetation period. The nannophytoplankton daily production at D_1 and D_2 is 1.7 g C/m^2 for the entire year, while for the vegetation period these values are 2.2 g C/m^2 for D_1 and 1.7 g C/m^2 for D_2. The total phytoplankton production during the vegetation period is 0.3 kg C/m^2 for D_1 and 0.2 kg C/m^2 for D_2. The nannophytoplankton production during the entire vegetation period is 0.3 kg C/m^2 at D_1 and 0.2 kg C/m^2 at D_2. The yearly production of the total phytoplankton is 0.6 kg C/m^2 for D_1 and 0.5 kg C/m^2 for D_2. The yearly production of the nannophytoplankton for D_1 and D_2 is 0.5 kg C/m^2. So on an annual basis the differences in production between the total phytoplankton and the nannophytoplankton, resulting from the floating leaves of the nymphaeids disappear. It is nevertheless a curious fact that the nannophytoplankton, separated from the larger particles, reached the same production level as the total phytoplankton including this nannophytoplankton fraction. The fact that on average the total phytoplankton community exists for more than 80% of nannophytoplankton (see Chapter 6, Section 6.2) can explain only part of this effect. The presence of high numbers of nannophytoplankton in the total phytoplankton community seems to reduce the total phytoplankton production.

Wetzel (1975) summarized production data from several freshwater bodies throughout the world. The production data from pond D of the Oude Waal easily fit into his 'eutrophic' category. Since the production data in Wetzel's table are based upon ^{14}C-measurements, we have to bear in mind that this method produces higher values (net production). Therefore the production data for pond D of the Oude Waal belong to the group of freshwater bodies with a somewhat lower (eu)trophic level (compare Nygaard, 1955; Megard, 1972; Likens, 1975; Wetzel, 1975) which can be distinguished within the total group of eutrophic freshwater bodies (mesotrophic water: 0.25 - 1.0 g C/m^2.day; eutrophic water: > 1.0 g C/m^2.day).

The shape of the phytoplankton biomass curves does not necessarily coincide with that of the phytoplankton productivity curve (Reynolds, 1984). In pond D of the Oude Waal the correlation between biovolume and productivity is poor (r^2 = 0.28 (D_1) or 0.36 (D_2)); the correlation is

better if chlorophyll-a is taken as a measure of biomass (r^2 = 0.54 (D_1) or 0.65 (D_2)). Hickman (1973), Bindloss (1974), Hickman & Jenkerson (1978), Hickman (1979), Robarts (1979), Hobson (1981) and many others have also found the correlation between chlorophyll-a and primary productivity to be insignificant and noted that this lack of correlation was probably due to the fact that the population density influenced the maximum possible productivity level by self-shading; according to these authors the dense algal populations influence the productivity level by reducing the available irradiance under water. In comparing the phytoplankton production in the open water area and that in the nymphaeid-dominated area it is found that the reduction in irradiance level under water indeed leads to a decrease in productivity level. But the phytoplankton biomass concentrations in pond D are - on average - not high enough to create situations in which self-shading could be expected. It seems more likely that it is the high tripton content of the water which causes a lower irradiance level here (cf. figs. 38 to 41).

In contrast to many other studies (Goldman, 1960, 1968; Hickman, 1973; Hickman & Jenkerson, 1978) no correlation was found between phytoplankton productivity and irradiance (whether incident or subsurface). This relationship is often found to be variable: a negative correlation has been reported by Waite (1970), while other investigators reported very poor (positive) correlations (Verduin, 1957; Efford, 1967; Dickman, 1969).

The pigment efficiency is correlated to the water temperature (table 25); this correlation is better for the phytoplankton in the open water area than for that in the nymphaeid-dominated area. There was no correlation between productivity and water temperature (table 25). The productivity levels at both sampling localities in pond D are apparently controlled by a complicated combination of factors, among which water temperature and irradiance are certainly not the most important ones. These controlling factors also include nutrients, the physiological state of the algae and water movements (retention time). Since the correlation between water temperature and pigment efficiency and that between irradiance and pigment efficiency are better for the phytoplankton in the open water area (D_1), than that in the nymphaeid-dominated area (D_2), the combination of phytoplankton productivity

controlling factors must be more complex for the nymphaeid-dominated area than for the open water area.

The mean phytoplankton renewal time for the total phytoplankton in the open water area (D_1) is 1.3 days for the full year and 0.9 days for the vegetation period; for the nannophytoplankton at D_1 the mean renewal time is 1.3 days for the entire year and 0.8 days for the vegetation period. The mean phytoplankton renewal time at D_2 is 1.5 days for the total phytoplankton, both for the entire year and for the vegetation period; for the nannophytoplankton at D_2 the mean renewal time is 1.1 days for the entire year and 0.8 days for the vegetation period. Comparable data from other water bodies are summarized in table 26.

Table 26. Phytoplankton renewal rates and renewal times for some selected fresh waters all over the world.

lake	renewal rate (day^{-1})	renewal time (days)	reference
alpine and pre-alpine lakes	0.02 - 10.42	0.1 - 2.5	Findenegg (1971)
Abbot's Pool	0.50 - 8.50	0.1 - 2.0 *	Hickman (1973)
Lake Kinneret	0.40 - 7.80	0.1 - 2.5	Berman & Pollinger (1974)
Lake Michigan	0.17 - 1.00 *	1.0 - 5.9	Parker et al. (1977)
Lake Bysjon	0.05 - 0.25	4.0 - 20.0	Coveney et al. (1977)
Lake Kinneret	0.07 - 0.13	7.9 - 13.7	Pollinger & Berman (1982)
Crose Mere	0.05	20.0 *	Reynolds (1984)
Lake Siggeforasjon	0.10 - 1.00	1.0 - 9.8	Heyman & Blomqvist (1984)

* these values have been converted from the original data, using an average light-day of 13 hours.

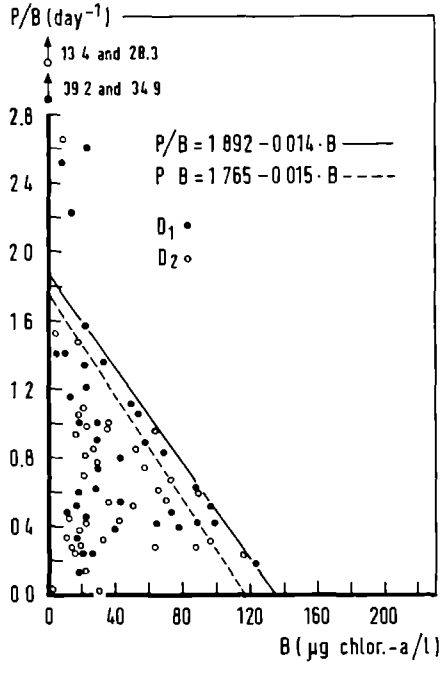
The renewal time for the nannophytoplankton community is always less than that for the total phytoplankton community. Renewal times as calculated here reflect upon the total phytoplankton or the nannophytoplankton community, both consisting of several algal species, each with its own renewal time. It is obvious that the phytoplankton community is in fact a mixture of species with low renewal times and species with high renewal times - at the moment of sampling. It is obvious that the most abundant species is not always the most productive one. Using an autoradiographic detection method (Watt, 1971), Stull et al. (1973) were able to identify the renewal time for individual algal species within a mixed phytoplankton community. The renewal times found in this study ranged from 0.09 days (*Oocystis lacustris*) to 380

days (*Navicula cryptocephala*) (calculated from the original data, assuming an average light-day of 13 hours). The dominant species - *Cyclotella meneghiniana* - had a calculated renewal time of 0.6 days. Renewal times can vary considerably even for one species, as has been illustrated for *Peridinium spp.* in Lake Kinneret by Pollingher & Berman (1982). Assuming that the renewal time of a phytoplankton community dominated by one or only a few taxa is the renewal time of the dominating taxa, table 27 indicates renewal times and rates for some taxa in pond D of the Oude Waal at those moments when they were dominant (i.e. constituted more than 80% of the total phytoplankton biovolume). This table shows, firstly, that the renewal time is dependent on the physiological state of the algae (which in turn depends on growth phase, nutrients, etc.) and, secondly, that the calculated renewal time is correlated to the chlorophyll-a content. In fact an inverse relationship exists between the algal renewal rate and the biomass (Koblenz-Mishke et al., 1976; Harris et al., 1983).

Table 27. Calculated renewal times, renewal rates and biomass for some phytoplankton samples from pond D of the Oude Waal, at the moment when the taxa indicated constituted more than 80% of the total phytoplankton biovolume.

sampling locality and sampling date		dominant taxa	renewal time (days)	renewal rate (day^{-1})	biomass (µg chlor.-a/l)
D_1	27 XI 1978	Cryptomonas spp.	2.1	0.47	12
	8 X 1979		5.6	0.18	123
	15 X 1979	Synura spp.	7.1	0.14	203
	22 X 1979		2.4	0.41	89
D_2	9 X 1978	Cyclotella meneghiniana	2.6	0.38	20
	23 X 1978	and	3.7	0.27	63
	30 X 1978	Stephanodiscus hantzschii	3.7	0.27	88
	18 XII 1978	Cryptomonas spp.	4.0	0.25	16
	8 X 1979		1.7	0.60	90
	15 X 1979	Synura spp.	4.2	0.24	117
	22 X 1979		1.8	0.57	70

The P/B-ratio versus B plot is illustrated for both sampling localities D_1 and D_2 in fig. 54 (total phytoplankton) and in fig. 55 (nannophytoplankton). In these plots a line can be constructed so that 90% of the points are situated beneath it. For the total phytoplankton this line is decribed by $P/B = 1.892 - 0.014B$ ($0 \leq B \leq 135$ µg chlor.a/l); for the nannophytoplankton it is described by $P/B = 2.25 - 0.018B$. Apart from the fact that these formulae allow the calculation of the maximum



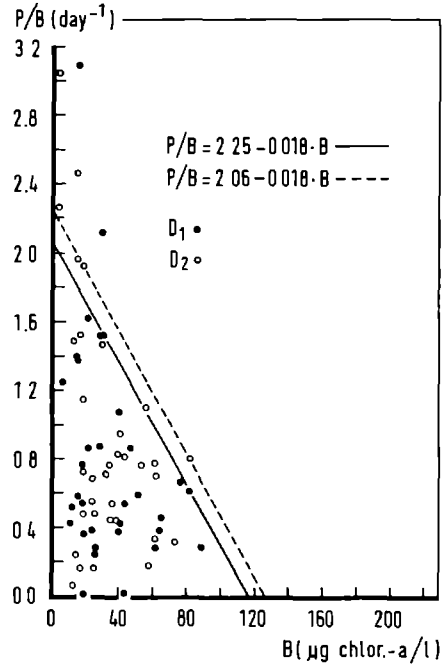


Fig. 54 (left). P/B versus B plot for the total phytoplankton in pond D of the Oude Waal. D_1= open water area; D_2= nymphaeid-dominated area. P = productivity; B = biomass.

Fig. 55 (right). P/B versus B plot for the nannophytoplankton in pond D of the Oude Waal. D_1= open water area; D_2= nymphaeid-dominated area. P = productivity; B = biomass.

possible phytoplankton productivity at pond D of the Oude Waal on the basis of a given chlorophyll-a content (within the ranges as indicated above), there are two other points of interest. In the first place it will be seen that all data from June to September for the nymphaeid-dominated area (D_2) are below the line P/B = 1.765 - 0.015B in fig. 54 (total phytoplankton). This implies that the same (total) phytoplankton biomass will have a much lower P/B-ratio and hence a much lower productivity at D_2 than at D_1, due to the interception of irradiance by the floating leaves. However, in fig. 55 all data from June to September for D_1 (the open water area) are below the line P/B = 2.06 - 0.018B. This implies that the same nannophytoplankton biomass must have a much higher P/B-ratio and hence a much higher productivity level at D_2 than at D_1. In the second place the highest concentration of points in the plots (particularly in the nannophytoplankton plot, fig. 55) is found at the left half of the plots, indicating a rapid turn-over, an efficient use of nutrients and a rather inefficient use of energy (Harris et al., 1983).

The efficiency as introduced by Hickman & Jenkerson (1978) and illustrated in figs. 50 and 51, gives little information about the quantum yield, i.e. the efficiency with which absorbed photons of PhAR are converted into photosynthetically stored energy (Tilzer, 1984). The quantum efficiency (the reverse of the quantum yield) is higher at D_2 than at D_1, especially during the vegetation period. In table 28 some literature data have been summarized, but since these data are all based on above-water irradiance, the values for the Oude Waal included in this table have also been calculated on the basis of above-water irradiance for the purpose of comparison (in table 24 the underwater irradiance at 15 cm below surface was used).

Table 28. Range of quantum efficiencies of phytoplankton as reported by various authors.

reference	range (%)	lake
Talling et al. (1973)	0.51 - 3.34	2 highly eutrophic Ethiopian lakes
Tilzer et al. (1975)	0.027 - 3.804	Lake Tahoe
Wetzel (1975)	0.01 - 3	an overall figure
Dubinsky & Berman (1976)	0.34 - 4.01	Lake Kinneret
Haynes & Hammer (1978)	0.027 - 3.804	7 saline lakes in Saskatchewan
present study	6.1 and 5.0	mean annual values for D_2 and D_1

Nevertheless the values for the Oude Waal are the highest ones in table 28. High (quantum) efficiencies (figs. 52 and 53) have been found for both sampling localities during the biomass and productivity increase of *Cyclotella meneghiniana/Stephanodiscus hantzschii* in October/November 1978, during that of *Stephanodiscus astrea* var. *minutula* in April and during that of *Synura spp.* in October 1979. Apparently these populations, up to that time fairly stable in their growth, became more and more effective in their energy utilization. As can be seen from the productivity efficiency index according to Hickman & Jenkerson (1978) (figs. 50 and 51), these efficiency increases are not due to an increase in phytoplankton biomass, but to an efficiency increase in the algal cells themselves.

The influence of the floating leaves of the nymphaeids upon the productivity efficiency of the phytoplankton can be seen clearly in fig. 52. The high efficiencies of the phytoplankton at D_2 as illustrated in this figure are solely the mathematical result of the use of low irradiance values in the denominator, since the underwater irradiance was used. In this context attention must be drawn to the confusing reports on the irradiance used in efficiency ratios. From the point of view of an investigator whose main interest is the place of a particular ecosystem within the total spectrum of ecosystems, arranged in order of their specific production efficiencies (Odum, 1971), incident irradiance (the above-water surface irradiance) is the most appropriate variable. But from the point of view of an investigator whose main interest is the energy storage efficiency of the organisms, the sub-surface irradiance (underwater irradiance) should be used in the formula. In spite of this, many studies use only incident irradiance (Hickman, 1976, 1979; Hickman & Jenkerson, 1978; Janus & Duthie, 1979).

8. PRODUCTIVITY INCUBATION EXCHANGE EXPERIMENTS

8.1. INTRODUCTION

The main difference between the open water area (D_1) and the nymphaeid-dominated area (D_2) in pond D of the Oude Waal is the presence of the nymphaeids at D_2. Consequently, one of the most obvious differentiating factors is the presence of floating leaves of the nymphaeids at D_2, and hence a lower underwater irradiance level there during the vegetation period (see fig. 19). These different irradiance levels at D_1 and D_2 must affect the phytoplankton primary productivity, particularly when communities persist at D_2 for a longer period, as is the case in times of very calm weather.

In order to investigate the reaction of the phytoplankton communities to a change in the irradiance level, incubation exchange experiments have been carried out, in which samples taken at D_1 were incubated both at D_1 and at D_2 and samples taken at D_2 were incubated both at D_2 and D_1.

8.2. PRODUCTIVITY

The results of the 6 experiments are listed in table 29. Although the differences are not significant in most cases, there is a tendency towards an increase in productivity when samples from D_2 were incubated at D_1 and a decrease in productivity when samples from D_1 were incubated at D_2.

Generally speaking, the productivity of algae, and even that of a mixed phytoplankton population, as a function of the irradiance can be represented as in fig. 56.

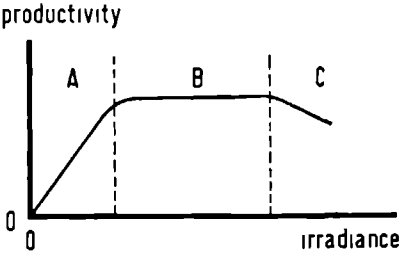


Fig. 56. General trend of the productivity of algae as a function of the irradiance. A = exponential phase, in which productivity is limited by irradiance; B = stationary phase, in which productivity is irradiance saturated; C = die-off phase, in which productivity is inhibited by irradiance.

Table 29. Productivity incubation exchange experiments in pond D of the Oude Waal. The productivity is given in mg O_2/l.h. The chlorophyll-a content (µg/l) and the underwater irradiance (E/m^2.h) are also given.
D_1 = open water area; D_2 = nymphaeid-dominated area.

A. Total phytoplankton

sampling locality	chlor.-a D_1	irrad. D_1	productivity D_1		chlor.-a D_2	irrad. D_2	productivity D_2	
incubation locality			D_1	D_2			D_1	D_2
date								
9 VII 1979	22.9	0.24	0.27	0.17	22.7	0.04	0.14	0.15
23 VII 1979	43.5	0.42	0.34	0.18	50.9	0.06	0.34	0.22
30 VII 1979	28.7	0.63	0.29	0.25	19.2	0.08	0.34	0.30
3 IX 1979	49.7	0.67	0.61	0.43	33.9	0.13	0.27	0.16
17 IX 1979	53.9	1.47	0.35	0.57	30.6	0.47	0.29	0.11
1 X 1979	-	1.03	0.49	0.39	-	0.55	0.21	0.19

B. Nannophytoplankton

sampling locality	chlor.-a D_1	irrad. D_1	productivity D_1		chlor.-a D_2	irrad. D_2	productivity D_2	
incubation locality			D_1	D_2			D_1	D_2
date								
9 VII 1979	15.7	0.24	0.20	0.06	15.2	0.04	0.28	0.20
23 VII 1979	38.6	0.42	0.09	0.12	38.8	0.06	0.15	0.17
30 VII 1979	20.5	0.63	0.34	0.28	17.3	0.08	0.24	0.30
3 IX 1979	30.6	0.67	0.43	0.61	29.7	0.13	0.38	0.36
17 IX 1979	29.5	1.47	0.68	0.65	23.6	0.47	0.14	0.38
1 X 1979	-	1.03	0.21	0.02	-	0.55	0.58	0.69

As the phytoplankton species composition at D_1 and D_2 is essentially the same - at least for the 6 dates on which the incubation exchange experiments were carried out - the productivity of the D_1 phytoplankton has in fact been determined at two irradiance levels (at D_1 and at D_2); the same is true for the D_2 phytoplankton. Hence it is possible to situate these two points (as well as the origin of the graphs) in the hypothetical productivity-versus-irradiance plot.

Fig. 57 shows the productivity-versus-irradiance plots for the total phytoplankton and nannophytoplankton incubation exchange experiments. In each plot the productivity of the phytoplankton sampled at D_1 or at D_2 and incubated at D_1 (open water area) is fixed at 100 % and the productivity at D_2 is given as the percentage of the productivity at D_1. The irradiance level at D_1 is also fixed at 100 %, and the irradiance level at D_2 given as the percentage of the irradiance level at D_1.

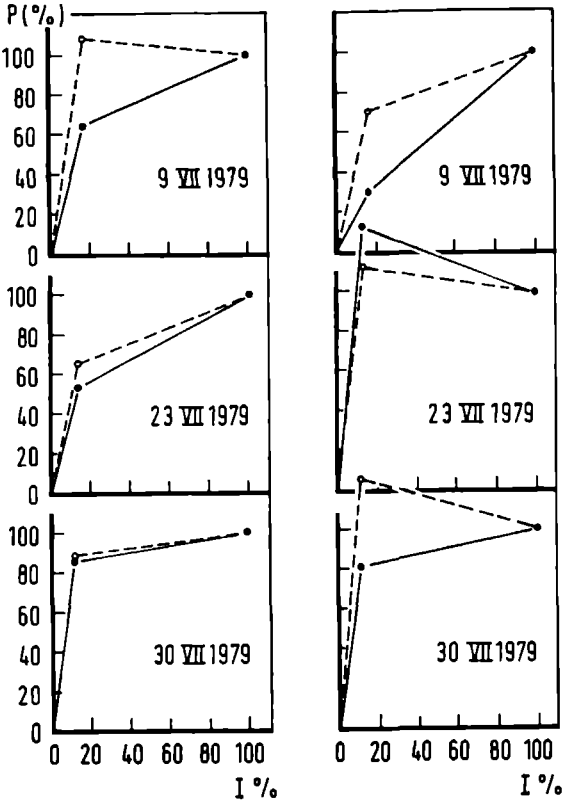


Fig. 57. Productivity-versus-irradiance plots for the phytoplankton incubation exchange experiments in pond D of the Oude Waal.
Left: total phytoplankton; right: nannophytoplankton.
Solid line: D_1 phytoplankton (open water); broken line: D_2 phytoplankton (nymphaeid-dominated).

Fig. 57 shows that the productivity of the total phytoplankton is in most cases not inhibited by the irradiance level at D_2 (nymphaeid-dominated area). Only the open-water total phytoplankton on 17 September seems to be irradiance-limited at D_1 (open water area), as is, to a lesser extent, the D_2 total phytoplankton on 9 July. On the other dates the total phytoplankton productivity is in its stationary phase, and the productivity at D_1 and that at D_2 are almost of the same magnitude; so the irradiance level does not influence the productivity to any great extent. In one situation the productivity of the total phytoplankton is still exponential (the D_2 total phytoplankton on 17 September); at that moment the total

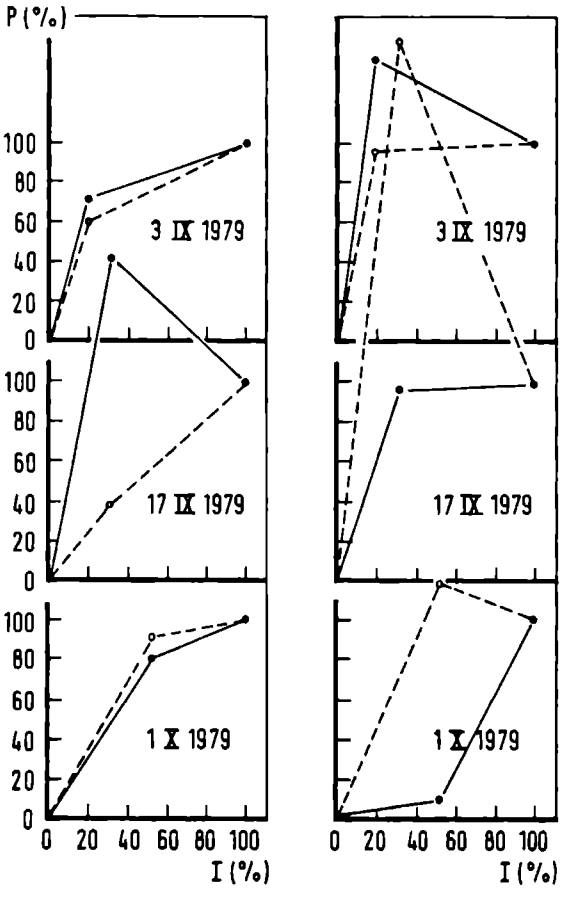


Fig. 57. (continued)

phytoplankton at D_2 is largely composed of *Aulacosira granulata*, which is obviously able to utilize the extra irradiance in the open water area to increase its productivity.

In many situations the productivity of the nannophytoplankton fraction reacts quite differently to the changes in irradiance level than does the total phytoplankton. On 23 July the nannophytoplankton at both sampling localities appears to be inhibited by the higher irradiance level in the open water area. On 30 July the D_2 nannophytoplankton is inhibited by the irradiance level in the open water area. On 3 September the D_1 nannophytoplankton is inhibited by the irradiance level at D_1, while the D_2

nannophytoplankton is at its irradiance-saturated level, while the D_2 nannophytoplankton is strongly inhibited by the irradiance level at D_1. On 1 October the D_2 nannophytoplankton is again inhibited by the higher irradiance at D_1, and the D_1 phytoplankton is strongly limited by the lower irradiance level at D_2 (nymphaeid-dominated area).

8.3. PIGMENT EFFICIENCY

The pigment efficiencies of the phytoplankton in the incubation exchange experiments are listed in table 30. These results confirm the results given in table 29; in other words, in these 6 experiments the differences in chlorophyll-a content of the phytoplankton at D_1 and at D_2 exert no influence on the reaction of the phytoplankton to changes in the irradiance level.

Table 30. Productivity incubation exchange experiments in pond D of the Oude Waal.
The pigment efficiency is given in mg O_2/mg chlor.-a.h.
D_1 = open water area; D_2 = nymphaeid-dominated area.

A. Total phytoplankton

sampling locality	D_1		D_2	
incubation locality	D_1	D_2	D_1	D_2
date				
9 VII 1979	11.8	7.4	6.1	6.6
23 VII 1979	7.8	4.1	6.7	4.3
30 VII 1979	10.1	8.7	17.7	15.6
3 IX 1979	12.3	8.7	8.0	4.7
17 IX 1979	6.5	10.6	9.5	3.6

B. Nannophytoplankton

sampling locality	D_1		D_2	
incubation locality	D_1	D_2	D_1	D_2
date				
9 VII 1979	12.7	3.8	18.5	13.2
23 VII 1979	2.3	3.1	3.7	4.4
30 VII 1979	16.6	13.7	13.9	17.4
3 IX 1979	14.1	19.9	12.8	12.2
17 IX 1979	23.0	22.0	5.9	16.1

The productivity incubation exchange experiments show that there is an effect of the irradiance interception by the floating leaves of the nymphaeids on the productivity of the phytoplankton. The total phytoplankton reacts differently to the change in irradiance level than the nannophytoplankton (fig. 57). In most situations the phytoplankton is at its irradiance-saturated productivity level. In some situations the results of a decrease in irradiance level clearly show that the previous (higher) irradiance level (solid lines in fig. 57) or the new (higher) irradiance level (broken lines in fig. 57) caused severe damage to the phytoplankton productivity, expressed as productivity inhibition by irradiance. This inhibition effect is found to occur more often in the nannophytoplankton fraction than in the total phytoplankton population.

Hence the nannophytoplankton seems well adapted to the lower irradiance level in the nymphaeid-dominated part of pond D, since short-term exposures to the higher irradiance level of the open water area of pond D result in a decrease in productivity.

The phytoplankton species composition at D_1 and D_2 is the same, except in the situation of 17 September, when the number of *Aulacosira granulata* cells in the nymphaeid-dominated part of pond D greatly exceeded the number of cells of this species in the open water area, resulting in a quite different reaction of the total phytoplankton to the change in irradiance level. In the other experiments the species composition at D_1 and D_2 was the same. As can be seen from the pigment efficiency (table 30), the chlorophyll-a content of the phytoplankton at D_1 and D_2 is of little importance for the general picture as this is illustrated in fig. 57. Hence, the different reactions to the change in irradiance by the phytoplankton at D_1 and at D_2 must be attributed to an adaptation of the algal cells, other than by regulation of the chlorophyll-a content per unit cell, as often reported in the literature (Steeman-Nielsen et al., 1962, Steeman-Nielsen & Jørgensen, 1968). The process of adaptation probably exceeds the four hours needed for the incubation of the phytoplankton samples. The results also show that the nannophytoplankton is much sooner inhibited by the higher irradiance level of the open water area and is consequently better adapted to the lower irradiance level of

the nymphaeid-dominated area. On the other hand some data suggest that the open water (nanno)phytoplankton populations are also inhibited by the high irradiance levels at that locality; they are probably able to avoid these high irradiance levels by migrating to the deeper parts of the pond, where the irradiance level is lower; enclosing in bottles has fixed them at a particular depth, where they normally would not stay for a longer period of time.

The irradiance levels given in table 29 suggest that on the four last dates photoinhibition could be expected, both for the total phytoplankton and for the nannophytoplankton fraction (Harris, 1978) in the open water area of pond D. This inhibition, however, is mainly found in the nanno-phytoplankton; the larger phytoplankton organisms are probably less sensitive to photoinhibition. The adaptation of the nannophytoplankton to the lower irradiance intensities at D_2, and in a few situations also to the high irradiance intensities at D_1, exceeds the four hours of incubation. If this adaptation was permanent, the weekly sampling program would also have traced it, for instance in the chlorophyll-a content per unit cell or per unit ashfree dry weight. This not the case. Hence the (nanno)phytoplankton populations in pond D are able to adapt to the irradiance level at that pond. This adaptation is better for the nannophytoplankton and particularly better to the lower irradiance levels. The time of adaptation is probably longer than 4 hours and less than 7 days (i.e. roughly 1 to 3 times the renewal time). These incubation exchange experiments allow the conclusion that adaptation of phytoplankton is primarily a survival strategy of the smaller algae and is a process which takes place within 1 to 3 generations of the phytoplankton communities, while it is also phased out within 1 to 3 generations.

9. PHYTOPLANKTON AS A COMPONENT OF THE NYMPHAEID-DOMINATED ECOSYSTEM; A GENERAL DISCUSSION

9.1. INTRODUCTION

Within a nymphaeid-dominated system several compartments can be distinguished, each with its own characteristic combination of species. Van der Velde (1980) distinguished 15 compartments within a nymphaeid-dominated system (fig. 58: A-O), and 16 structural elements, which are distinguished according to the mode of utilization of space. Structural elements in the system which contribute to the primary production are: a) the nympnaeids themselves, b) the associated macrophytes, c) the epiphyton and d) the phytoplankton. Of these elements only the phytoplankton is able to photosynthesize all year round.

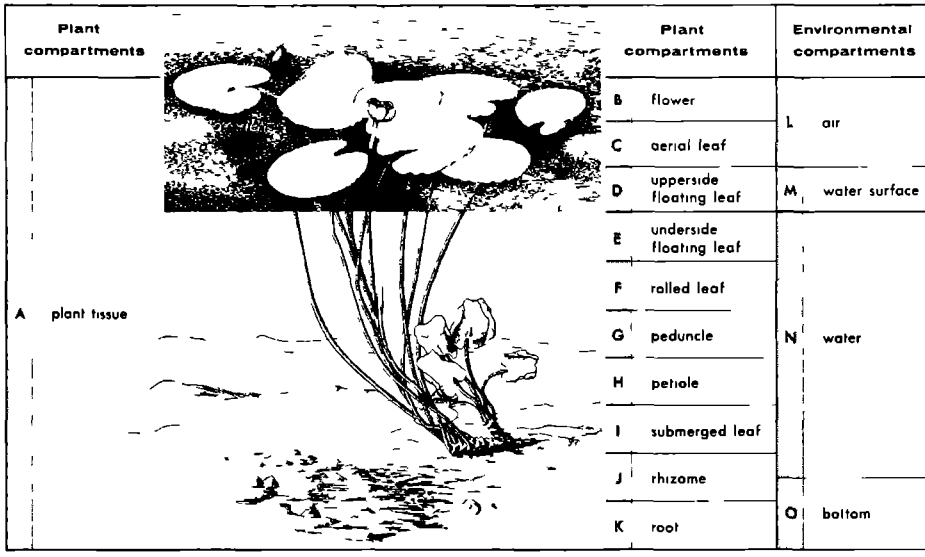


Fig. 58. Various compartments which can be distinguished in a nymphaeid-dominated system. (from Van der Velde, 1980).

Changes in the phytoplankton biomass are the result of phytoplankton primary production, the input of phytoplankton biomass from elsewhere (resuspension of settled phytoplankton, input of released epiphytes, input of phytoplankton from other parts of the water body) and the output of phytoplankton biomass (by grazing, sedimentation, death and transportation to other parts of the water body). Changes in phytoplankton species composition are determined by tolerance for environmental conditions, abiotic as well as biotic.

In the next section both groups of environmental conditions will be discussed to illustrate the changes in phytoplankton species composition, the phytplankton biomass development and the differences between the open water phytoplankton and the phytoplankton in the nymphaeid-dominated area. In the last section of this chapter perspectives for further research will be discussed.

9.2. PHYTOPLANKTON AND ITS ENVIRONMENT

The abiotic environment of the phytoplankton in the nymphaeid-dominated system of the Oude Waal consists in the first place of the aquatic environment itself. Since planktonic algae are autotrophic, their growth depends on dissolved nutrients, irradiance level and water temperature. The water temperature in the Oude Waal follows roughly the temperature of the air above the water surface, but rapid fluctuations are not followed. The differences in water temperature between the open water areas and the nymphaeid-dominated areas were too small to be detected. In a deeper part of the system, as for instance at locality F_1, the sheltered situation of the locality allows the development of a temperature gradient in summer. Phytoplankton samples taken from above and below the thermocline did not reveal important differences in species composition. The biomass of the phytoplankton however showed an increase towards the deeper parts of the pond (fig. 59). The phytoplankton biomass clearly settles down and in the stratification period the settled biomass cannot reach the upper layers of the pond and will stay in the hypolimnion, where the irradiance level is too low to maintain phytoplankton growth (the irradiance level below 5 m is on average less than 0.5 percent of the incident irradiance). In this way the hypolimnion serves as a biomass trap, and consequently as a nutrient trap. As can be seen from figs. 60, 61 and 62 a large portion

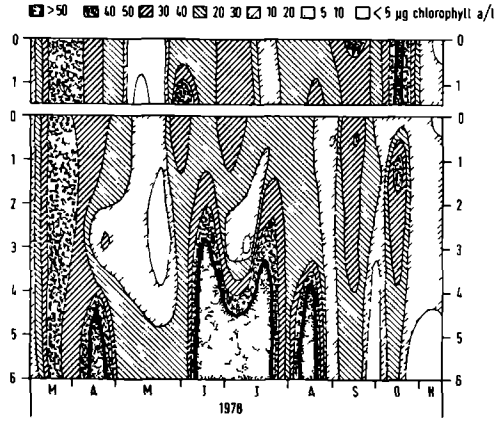


Fig. 59. Depth-time diagrams of seasonal developments in the concentrations of chlorophyll-a in pond F of the Oude Waal. Period: May to November 1978. Concentrations in µg/l. Above figure: F_2 (nymphaeid-dominated area); lower figure: F_1 (open water area).

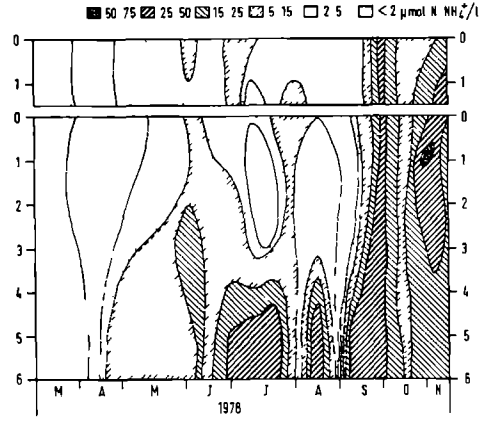


Fig. 60. Depth-time diagrams of seasonal developments in the concentrations of $N\text{-}NH_4^+$ in pond F of the Oude Waal. Period: May to November 1978. Concentrations in µmol/l. Above figure: F_2 (nymphaeid-dominated area); lower figure: F_1 (open water area).

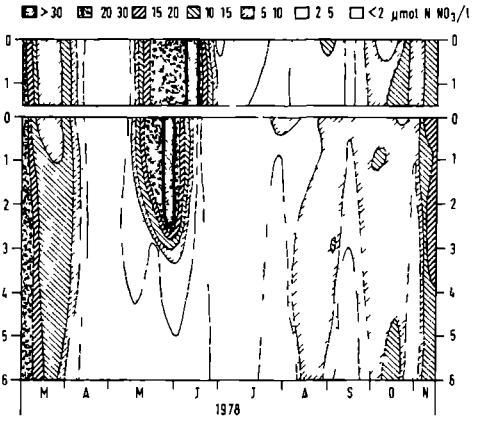


Fig. 61. Depth-time diagrams of seasonal development in the concentrations of $N\text{-}NO_3^-$ in pond F of the Oude Waal. Period: May to November 1978. Concentrations in µmol/l. Above figure: F_2 (nymphaeid-dominated area); lower figure: F_1 (open water area).

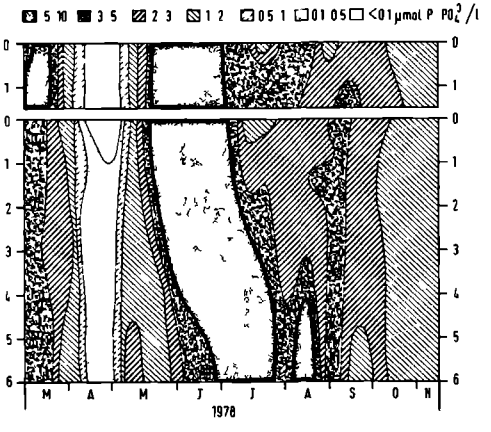


Fig. 62. Depth-time diagrams of seasonal developments in the concentrations of $P\text{-}PO_4^{3-}$ in pond F of the Oude Waal. Period: May to November 1978. Concentrations in µmol/l. Above figure: F_2 (nymphaeid-dominated area); lower figure. F_1 (open water area).

of the N- and P-compounds which are fixed by the phytoplankton, transported to the deeper parts of the pond and there released, is not transported back to the upper water layers during the period of vertical mixing of the water layers in autumn.

In the shallower parts (F_2, D_1 and D_2) the situation is different, as can be seen from the upper figures in figs. 59, 60, 61 and 62. A complete mixing of the water masses prevents stratification, even in summer, when the floating leaves of the nymphaeids (at D_2 and F_2) reduce the influence of wind and wave action. But even in these shallower parts of the Oude Waal a considerable part of the nutrients released by phytoplankton will be absorbed by the sediments. These nutrients will be available to the rooted macrophytes (Best & Mantai, 1978; Barko & Smart, 1980; Carignan & Kalff, 1980). Brock et al. (1983a) calculated that *Nymphoides peltata*, the dominant macrophyte in the Oude Waal, absorbed over 80% of its phosphorus requirements from the sediments. The senescence of floating leaves takes place during the entire growing season (Brock, 1984). The floating leaves of *Nuphar lutea* and *Nymphaea alba*, the two other important macrophytes, also decay continuously during the growing season (Van der Velde, 1980; Van der Velde & Peelen-Bexkens, 1983). In their studies of the natural breakdown of *Nymphoides peltata*, Brock et al. (1983a) showed that losses of biomass due to tissue decay were continuous from the start of the vegetation period. They postulated that there must be a flux of nitrogen and phosphorus from the decomposing *Nymphoides* to the water compartment, but could not detect clear differences in concentrations of dissolved nitrogen and phosphorus compounds between localities with and without *Nymphoides*. Brock et al. (1983a) therefore assumed that a considerable exchange of water occurred between localities with and without *Nymphoides*.

The present study has also shown that no clear differences in nutrient concentrations in the water exist between localities in the Oude Waal with and without nymphaeids. The species composition of the phytoplankton at both localities was identical. During the period from May to October 1979 the ashfree dry weight of the seston was higher in the nymphaeid-dominated area than in the open water area. This higher organic weight in the nymphaeid-dominated area resulted to a large extent from the nymphaeids themselves (Brock, 1984). The higher biovolumes of the phytoplankton in

the nymphaeid-dominated area, particularly during October 1979, indicate that in that period the phytoplankton biomass in this area was somewhat higher than in the open water area. The most likely explanation is that the smaller autotrophs such as phytoplankton and epiphytic algae absorb the nutrients immediately after they have been released by the decaying nymphaeids. This is also in agreement with Landers (1982), who found that in enclosures, in which water exchange was eliminated, nitrogen and phosphorus levels increased in waters surrounding the senescing aquatic macrophytes, resulting in an increase of phytoplankton and epiphytic algae biomass. In this respect it is important to know that several authors have actually proved the utilization by the epiphyton of dissolved organic products released by various macropnytes (Linskens, 1963; Fitzgerald, 1969; Allen, 1971; Harlin, 1973 and 1975; McRoy & Goering, 1974; Langlois, 1975).

The assumption of Brock et al. (1983a) that there must be a considerable exchange of water between the open water areas and the nymphaeid-dominated areas thus also reflects upon the phytoplankton species composition. The presence of nymphaeids however will have effects on the functioning of these phytoplankton communities. In the case of the chlorophyll-a content of phytoplankton organisms good examples have been given in Chapter 6. *Pandorina morum* shows a high chlorophyll-a content in the open water area of pond D, whereas in the nymphaeid-dominated area of that pond its chlorophyll-a content is lower. Consequently the productivity of these phytoplankton communities, dominated by *Pandorina morum*, will be lower in the shaded areas. The higher chlorophyll-a content in the open water area of pond D during the *Synura spp.* bloom in October 1979, compared to that in the nymphaeid-dominated area, is also - indirectly - caused by the nymphaeids. In this situation the accumulation of litter in the nymphaeid-dominated area will inhibit the accumulation of chlorophyll-a in the phytoplankton by lowering the irradiance level. Turbulence and resuspension of sedimented material will thus greatly influence the irradiance level in the nymphaeid-dominated area and hence the phytoplankton community structure and functioning.

The effect of zooplankton grazing upon the phytoplankton species composition and biomass has not been studied in the Oude Waal. Field observations show that in the period of May to October the zooplankton

communities between the nymphaeids are very complex and can reach a high biomass. Especially *Cladocera* and *Rotatoria* are found among the nymphaeids, while *Ciliata*, *Ostracoda* and *Harpacticoida* are found near the bottom of the nymphaeid-dominated area. In the nymphaeid stands *Cladocera* particularly have been seen in dense patches. For these places the effect of grazing certainly should be noticeable in phytoplankton biomass data, but in the mixed samples (see Chapter 3) these local effects are not found back. It is assumed that the grazing pressure in the nymphaeid-dominated area is mainly directed at the epiphytes, as the zooplankton patches are mostly seen near the nymphaeids themselves.

The few differences in structure and functioning of the phytoplankton communities between the open water area and the nymphaeid-dominated area almost disappear if the yearly production of both areas is calculated. The daily gross production of the phytoplankton in the open water area of pond D (D_1) is 1.7 kg C/m^2, while in the nymphaeid-dominated area of that pond (D_2) it is 1.4 kg C/m^2. The daily net productivity is somewhat lower, viz. 1.6 kg C/m^2 (D_1) and 1.3 kg C/m^2 (D_2). The surface areas of D_1 and D_2 are 9500 m^2 and 8000 m^2 respectively (table 4, Chapter 4), so the annual production of the phytoplankton in pond D is 25.6 ton C.

In an ecological investigation in which values are derived as above, it is tempting to compare these values with comparable data from other studies. Wetzel (1975) gives a summary of phytoplankton production values for several freshwater bodies of various trophic degrees. Judging by this author's data the Oude Waal is very well comparable with other eutrophic freshwaters. But is is even more tempting to compare the phytoplankton production data with similar data for the nymphaeids. The best available data have been published by Brock et al. (1983b). These production data regard *Nymphoides peltata*, the dominant nymphaeid in the Oude Waal. Brock et al. (1983b), however, studied a different water body and their study was carried out in a different year than the phytoplankton studies presented here. According to Brock et al. (1983b) the net annual production of *Nymphoides peltata* was 1.036 kg ashfree dry weight/m^2. According to the same investigators the mean organic carbon content for *Nymphoides peltata* was 52%. So the net annual production of *Nymphoides peltata* is 0.55 kg C/m^2. Using the data from table

4 (Chapter 4) for the area in which the nymphaeids occur in pond D (8000 m^2), the production budget for pond D, which may be seen as illustrative for the entire Oude Waal, can be given. In pond D the annual production of *Nymphoides peltata* is 4.4 ton C, while the annual production of the phytoplankton is 25.6 ton C, thus exceeding the nymphaeid net production nearly 6 times; if pond D was filled entirely with *N. peltata* this would be 7.4 times (1.3 kg C/m^2 divided by 0.55 kg C/m^2).

9.3. PERSPECTIVES FOR FURTHER RESEARCH

This last section would seem the right place to indicate some of the many possibilities for further research which emerge from the present study. Several questions remain to be answered.

In the context of the nymphaeid project the time has come to start a fully integrated study of all autotrophic structural elements in the nymphaeid-dominated ecosystem at the same time. This is the only way to obtain comparable production data. In this light the present data must be seen as guidelines. Furthermore it is not clear whether other nymphaeid-dominated freshwater bodies, which are not influenced by a river as in the case of the Oude Waal, or which are geomorphologically completely different, will show the same production values for phytoplankton and nymphaeids. In this respect the nutrient balance could also be completely different in those waters. The link between nymphaeids and phytoplankton is particularly clear in the decaying process of the nymphaeids. Special attention should be paid to this phenomenon from the point of view of the phytoplankton. Bioassays, such as carried out by Van Donk (1983), are one possibility for tracing the effects of nutrients released from the nymphaeids on the planktonic algae. A better, but more expensive, way to investigate these effects is the use of enclosures, as was done by Landers (1982).

The link between zooplankton and phytoplankton has not yet been studied. As was already mentioned in the previous section, zooplankton studies in the nymphaeid-dominated systems should be better linked up with the study of epiphytes.

Outside the nymphaeid project the present phytoplankton-centred studies provide a good starting-point for two other lines of aquatic

ecological research. The first line is pure phytoplankton ecology. Since Hutchinson (1967) published his review on phytoplankton associations, only a few publications have followed in which more light was thrown on this subject. Hutchinson (1967) defined 13 phytoplankton associations and encouraged a further elaboration of these 13 associations. There is indeed a great need for this, since for instance the association characteristic of the Oude Waal (Chapter 6) is intermediate between 2 associations mentioned by Hutchinson (1967): 'eutrophic diatom plankton' and 'eutrophic chlorococcal plankton'. In the Netherlands Schroevers & Dresscher (1977) published a typology of fresh and brackish waters on the basis of microphytes. They divided the Netherlands into seven hydrobiological districts (fig. 63), in a similar way as was done for the macrophytes by Van Soest (1925, 1929). Schroevers & Dresscher (1977) also gave lists of microphytes characteristic for the many different types of surface waters in these districts. In this light the present study must be seen as an elaboration of one of the types that Schroevers & Dresscher (1977) distinguished in their district 2 ('main rivers and immediate surroundings'): 'very old cut-off river branches'. For the purpose of drafting management guidelines for surface waters one needs to have a well-constructed description of the structure (and functioning) of the aquatic ecosystems in question. Description of the structure of phytoplankton communities is one of the major elements in those systems and for that reason alone more types of water bodies will have to be described in detail. As already mentioned in Chapter 5, this should be based on an at least weekly sampling programme (Roijackers, 1981d). These investigations could use the typology presented by Schroevers & Dresscher (1977) as a guideline. A great deal of research is already being carried out by Provincial authorities and water boards, but the integration and interpretation of these species lists will be the next step in the effort to present a detailed classification of the phytoplankton communities in Dutch surface waters, in the sense of Hutchinson (1967). Such a classification could be used to enlarge and improve the scheme of successional pathways in surface waters of different trophic status as presented by Reynolds (1984). This would certainly help us to understand the mechanisms of seasonal change in phytoplankton communities.

A second line of aquatic ecological research concentrating on the

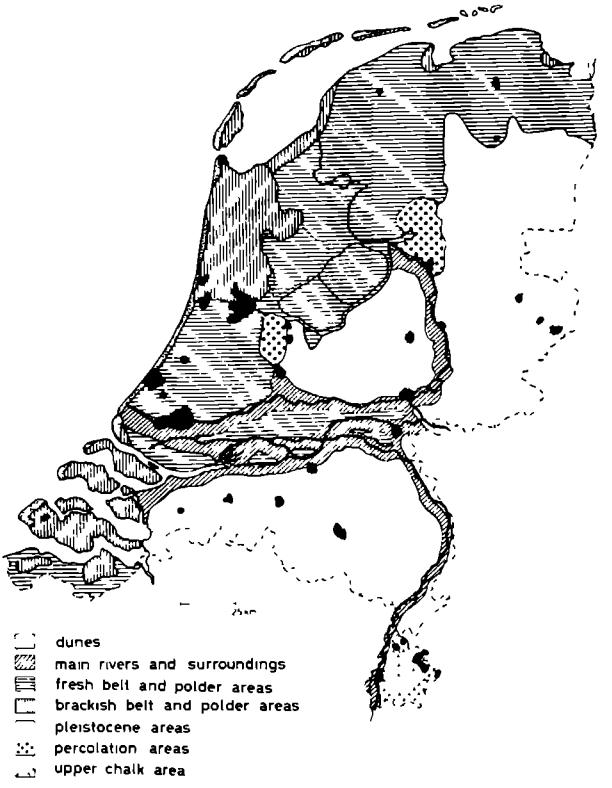


Fig. 63. Hydrobiological districts in the Netherlands (after Schroevers & Dresscher, 1977).

phytoplankton is again linked with macrophytes and with management problems. In many nutrient-enriched shallow waters macrophytes are disappearing and phytoplankton blooms appear instead. Philips et al. (1978) presented a new hypothesis on the mechanisms behind this macrophyte decline. In their opinion macrophytes suppress phytoplankton by organic secretions. In eutrophicated waters the growth of epiphytes and filamentous algae will suppress the macrophyte growth by shading. As a result, the rate of secretion of phytoplankton suppressants decreases, as does the uptake of nutrients from the water by macrophytes; hence phytoplankton growth will increase, resulting in a further decrease of the macrophytes.

Van Vierssen et al. (1985) substantiated this hypothesis and included the effects of management. In both models the influence of irradiance (shading) and available nutrients on the macrophyte development is important. It is therefore necessary to include both these factors in the above-mentioned theories. In this respect special attention should be paid to the role of the sediment in the system, particularly since macrophyte-dominated systems are shallow, and wind-induced turbulence will certainly increase resuspension of settled material. Macrophyte decline can occur in any nutrient-enriched shallow aquatic ecosystem. As already explained in the Introduction (Chapter 1), the Oude Waal for instance could be seen as one phase in the succession series of aquatic macrophytes. An enrichment with nutrients could easily change this succession. A thorough knowledge of the nutrient interactions between sediment, water and autotrophs, together with a thorough knowledge of the influence of macrophytes, epiphytes, plankton and (re)suspended material on the underwater light climate is needed to give a starting-point for adequate management.

SUMMARY

The phytoplankton of the Oude Waal, an oxbow lake of the river Waal, situated in the Ooypolder near Nijmegen, was studied for a number of years. The Oude Waal is situated in the river forelands and is very little influenced by the river Waal. The Oude Waal system is characterized by a dominance of nymphaeids, particularly *Nymphaea alba*, *Nuphar lutea* and *Nymphoides peltata*. The research project concerned itself with a number of specific questions. The first aim of the study was to make an inventory of phytoplankton taxa occurring in the Oude Waal. A second aim was a determination of the primary production of the Oude Waal phytoplankton, while a third was a study of the role of the nannophytoplankton in the whole of the phytoplankton communities, both as regards structure (species composition, biomass) and as regards functioning (variations in biomass and productivity). A final aim was to study the influence of the nympnaeids on the phytoplankton communities, again as regards both structure and functioning of the communities.

In order to gain some insight into the species composition of the phytoplankton in the various distinguishable parts of the Oude Waal, a comparative study of the species composition in five different parts of the area was carried out in the first half of 1977, on the basis of monthly sampling. In addition to the phytoplankton species composition, the chemical composition of the water body was also studied. Since the Oude Waal had largely fallen dry in the summer of 1976, this sampling period also meant a registration of the effects of a rising water level on the exchange of phytoplankton taxa, as well as on the differences in the chemical composition of the water body. This study showed that the five different - and initially isolated - research localities in the Oude Waal each developed their own species compositions, which were however completely blended when maximum water levels were reached in February 1977, as the river Waal overflowed its banks and flooded the entire Oude Waal area. After this month, the water level in the Oude Waal fell steeply, to a reasonably stable level, at which the exchange of phytoplankton organisms between the various parts of the system was minimized.

Subsequently, from May 1977 to April 1978, a more detailed study was made of one of the five original research localities, viz. pond F, a fairly deep part of the Oude Waal, dominated by nymphaeids in its shallower part (F_2). This part of the research project concentrated on registration of the phytoplankton species composition and biomass, while the water chemistry was studied with the same (i.e. weekly) frequency. A comparison between the nymphaeid-dominated area (F_2) and the open water area (F_1) in this study showed the influence of the nymphaeids on the species composition to be negligible. Neither did the phytoplankton biomass at the two research localities show any important differences. However, during the period of maximum development of the nymphaeids, the chlorophyll-a content of the phytoplankton underneath these macrophytes was lower than that in the open water area. But the fact that there was also a considerable difference in water depth between the open water area and the nymphaeid-dominated area made it impossible to conclude that a direct relation existed with the presence of the nymphaeids.

For this reason, the study was repeated in the period of October 1978 to October 1979 in pond D, where the depth of the open water area (D_1) was equal to that of the nymphaeid-dominated area (D_2). This study also included a determination of the primary productivity of the phytoplankton, as well as related parameters such as pigment efficiency, quantum efficiency, turnover and productivity efficiency. Furthermore, the importance of the nannophytoplankton was included in this study. The chemical composition of the water of the two localities was found to be identical. Chlorophyll-a contents in the nymphaeid-dominated area were found to be lower than those in the open water area during the vegetation period, while biovolume and ash-free dry weight were slightly higher in the nymphaeid-dominated area during this same period. In addition, the ash-free dry weight in the nymphaeid-dominated area showed major fluctuations during the vegetation period. This leads to the hypothesis that the phytoplankton in D_2 can produce a higher biomass (biovolume), utilizing the nutrients which become available through the continuous decay of the nymphaeids (the ash-free dry weights also include smaller remains of the higher aquatic plants). Since the actual concentrations of these nutrients in the water body showed no increased level, it must be assumed that the phytoplankton immediately takes up these nutrients and converts them into new biomass. The phytoplankton

communities consist for over 30% of Chlorophyta, for 30% of Bacillario-phyta and for 25% of Chrysophyta; in addition to these groups, Crypto-phyta also play an important role as far as biomass is concerned. In the nannophytoplankton, which on average includes 80% of the taxa, as well as of the total biomass, most of the taxa belong to the Chlorophyta, Chryso-phyta and also Bacillariophyta, while five groups together make up 94% of the biomass. It is possible to distinguish a typical combination of phytoplankton taxa which are present in the Oude Waal for the larger part of the year (61 - 100% of the samples). A number of the species in this combination act as dominants, some of which can be qualified as rapid growers, while others grow more slowly in periods of environmental stability. The productivity of the phytoplankton at D_1 was found to differ little from that in D_2 (on average 0.33 mg O_2/l.h for D_1 and 0.27 mg O_2/l.h for D_2), while for the nannophytoplankton the values for the two locations are practicaly identical (0.27 and 0.28 mg O_2/l.h respectively). The turnover rate for the total phytoplankton community is higher in the open water area (D_1) than in the nymphaeid-dominated area (D_2); for the nannophytoplankton (80% of the total phytoplankton biomass), the turnover rate is higher at D_2 than at D_1, another indication of the rapid fixation of nutrients released in the decay of the nymphaeids. Both the productivity efficiency and the quantum efficiency are higher at D_2 than at D_1, both for the nannophytoplankton and for the total phytoplankton; the pigment efficiencies are identical for D_1 and D_2, again for both phytoplankton fractions.

Productivity incubation exchange experiments were used to test whether the phytoplankton reacts immediately to changes in the irradiance level or whether it is adapted to a specific level. These experiments showed that, in the field, the nannophytoplankton is able to adapt to an existing irradiance level; this adaptation is not effected through changes in the chlorophyll-a content per cell, and it is achieved only after more than four hours. The adaptation is not permanent; it can be reversed within seven days.

The annual net production of the phytoplankton in pond D is 25.6 tonnes of C; this figure has been corrected for the fact that only part of the pond houses nymphaeids. The annual production of the dominant nymphaeid in pond D, *Nymphoides peltata*, is to be found in the literature:

0.55 kg C/m^2; hence in pond D the annual net production of this macrophyte must be 4.4 tonnes of C. This shows that the phytoplankton production on an annual basis is about six times that of *Nymphoides peltata*. Even if *Nymphoides peltata* covered the entire pond, the annual production of the phytoplankton would still be 2.4 times that of *Nymphoides peltata*.

ONDERZOEK NAAR HET FYTOPLANKTON IN EEN DOOR NYMPHAEIDEN GEDOMINEERD SYSTEEM

SAMENVATTING

Van de Oude Waal, een oude rivierarm van de Waal, gelegen in de Ooypolder bij Nijmegen in de uiterwaarden en vrijwel afgesloten van de invloeden van de Waal, is het fytoplankton gedurende een aantal jaren bestudeerd. Het Oude Waal systeem wordt gekenmerkt door een dominantie van nymphaeiden, met name *Nymphea alba*, *Nuphar lutea* en *Nymphoides peltata*. Aan het onderzoek waren een aantal specifieke vragen verbonden. Een eerste punt van onderzoek was de inventarisatie van de in de Oude Waal voorkomende fytoplankton taxa. Een tweede punt van onderzoek was het vaststellen van de primaire produktie van het fytoplankton in de Oude Waal. Een derde punt van onderzoek betrof het aandeel van het nannofytoplankton in de totale fytoplankton gemeenschappen, zowel qua struktuur (soortensamenstelling, biomassa), als qua funktioneren (wisselingen in de biomassa, wisselingen in de produktiviteit). Een laatste punt van onderzoek betrof de invloed van de nymphaeiden op de fytoplanktongemeenschappen, eveneens voor wat betreft de struktuur en het funktioneren van de gemeenschappen.

Om een inzicht te krijgen in de soortensamenstelling van het fytoplankton in de diverse te onderscheiden delen van de Oude Waal, is in de eerste helft van 1977 een vergelijkend onderzoek naar de soortensamenstelling in vijf verschillende delen van de Oude Waal uitgevoerd, op basis van een maandelijkse bemonstering. Naast de fytoplankton soortensamenstelling is ook de chemische samenstelling van de watermassa bestudeerd. Omdat de Oude Waal in de zomer van 1976 voor het merendeel droog was gevallen, was deze onderzoeksperiode tevens een registratie van de effekten van een rijzende waterspiegel op de onderlinge uitwisseling van fytoplanktontaxa, alsook op de verschillen in chemische samenstelling van de watermassa. Uit dit onderzoek is naar voren gekomen dat de vijf verschillende - aanvankelijk geïsoleerde - onderzoekslocaties in de Oude Waal een geheel eigen soortensamenstelling ontwikkelden, dewelke volkomen gemengd werd bij het bereiken van de hoogste waterstanden in februari 1977, toen de Waal buiten zijn oevers

trad en de gehele Oude Waal overstroomde. Vanaf die periode daalde de waterspiegel in de Oude Waal snel, tot een vrij stabiel niveau, waarbij de uitwisseling van fytoplanktonorganismen tussen de verschillende delen van de Oude Waal minimaal werd.

Van mei 1977 tot april 1978 werd vervolgens een diepgaander onderzoek verricht op één van de vijf oorspronkelijke onderzoekslocaties en wel in kolk F, een wat diepere doorbraakkolk van de Oude Waal, waar in het ondiepere deel (F_2) nymphaeiden overheersten. Bij dit onderzoek stond de registratie van de fytoplanktonsoortensamenstelling en -biomassa centraal en werd tevens de waterchemie met dezelfde frequentie (wekelijks) onderzocht. Uit dit onderzoek kwam naar voren dat de invloed van de nymphaeiden op de soortensamenstelling minimaal was, wanneer de door nymphaeiden gedomineerde zone (F_2) vergeleken werd met de open water zone (F_1). Ook de fytoplanktonbiomassa vertoonde op beide onderzoekslocaties weinig verschillen. De chemische samenstelling van de watermassa was voor F_1 gelijk aan die van F_2. Het gehalte aan chlorofyll-a was onder de nymphaeiden echter lager dan in de open water massa gedurende de maximale ontwikkeling van deze makrofyten. Het feit dat er ook een groot verschil in diepte was tussen de open water zone en de door de nymphaeiden gedomineerde zone, sloot een direkt verband met de aanwezigheid van de nymphaeiden uit.

Gedurende de periode oktober 1978 tot oktober 1979 werd daarom het onderzoek herhaald in kolk D, waar de diepte van de open water zone (D_1) gelijk was aan die van de door nymphaeiden gedomineerde zone (D_2). In dit onderzoek werd ook de primaire produktiviteit van het fytoplankton bepaald, evenals de daaraan te koppelen variabelen als pigment efficientie, quantum efficientie, turn-over en produktiviteits efficientie. Bovendien werd in dit onderzoeksjaar het belang van het nannofytoplankton in het onderzoek betrokken. De chemische samenstelling van de beide watermassa's was identiek. De chlorofyll-a gehalten waren in de door nymphaeiden gedomineerde zone lager gedurende de vegetatieperiode vergeleken met de open water zone, terwijl het biovolume en het asvrij drooggewicht juist in die periode iets hoger waren in de door de nymphaeiden gedomineerde zone. Het asvrij drooggewicht in de door de nymphaeiden gedomineerde zone fluctueerde bovendien sterk gedurende de vegetatieperiode. Dit leidt tot de veronderstelling dat het fytoplankton op D_2 een hogere

biomassa kan vormen (biovolume), gebruik makend van de nutriënten die bij de voortdurende afbraak van de nymphaeiden (asvrij drooggewichten omvatten ook kleinere resten van de hogere waterplanten) vrijkomen. Aangezien de aktuele concentraties van deze nutrienten in de watermassa niet verhoogd waren, moet verondersteld worden dat het fytoplankton deze nutriënten direkt weer opneemt en in nieuwe biomassa omzet. De fytoplanktongemeenschappen omvatten voor ruim 30% Chlorophyta, voor 30% Bacillariophyta en voor 25% Chrysophyta; qua biomassa spelen naast deze groepen ook de Cryptophyta een belangrijke rol. Voor het nannofytoplankton, wat gemiddeld 80% van de taxa alsook van de biomassa omvat, zijn de meeste taxa te vinden onder de Chlorophyta, Chrysophyta en ook wel de Bacillariophyta, terwijl 5 groepen tesamen 94% van de biomassa vormen. Er is een typische combinatie van fytoplanktontaxa te onderscheiden, die gedurende het merendeel van een jaar (61-100% van de monsters) in de Oude Waal aanwezig is. Hierbij treden sommige soorten als dominanten op, deels te rekenen tot de snellere groeiers en deels te rekenen tot de wat langzamere groeiers in de perioden van stabiliteit in het milieu. De produktiviteit van het fytoplankton in D_1 verschilt niet veel van de produktiviteit van het fytoplankton in D_2 (gem. 0,33 mg O_2/l.u voor D_1 en 0,27 mg O_2/l.u voor D_2) en is voor het nannofytoplankton zelfs vrijwel gelijk (resp. 0,27 en 0,28 mg O_2/l.u) op beide monsterlokaties. De verdubbelingssnelheid van de totale fytoplanktongemeenschap is in de open water zone (D_1) hoger dan in de door nymphaeiden gedomineerde zone (D_2); de verdubbelingssnelheid van het nannofytoplankton (80% van de totale fytoplanktonbiomassa) is op D_2 hoger dan op D_1, opnieuw een indikatie voor de snelle vastlegging van de bij de afbraak van de nymphaeiden vrijkomende nutriënten. Zowel de produktiviteitsefficiëntie als de quantumefficiëntie zijn op D_2 hoger dan op D_1, zowel voor het nannofytoplankton als het totale fytoplankton; de pigmentefficiëntie is op D_1 gelijk aan die op D_2, eveneens voor beide fytoplanktonfrakties.

Met behulp van produktiviteits-incubatie uitwisselingsproeven is getest of het fytoplankton direkt reageert op de veranderingen in de instralingsintensiteit, of aangepast is aan een bepaalde instralingsintensiteit. Uit deze experimenten bleek dat in het veld het nannofytoplankton in staat is zich aan te passen aan een bestaande instralingsintensiteit; deze aanpassing is niet een aanpassing via ver-

anderıng van het chlorofyll-a gehalte per cel, en treedt pas na meer dan vıer uur op. Daar tegenover staat dat de adaptatıe nıet permanent ıs en bınnen zeven dagen weer ongedaan gemaakt kan worden.

In kolk D ıs de jaarlıjkse netto produktıe van het fytoplankton 25,6 ton C; hıerbıj ıs rekenıng gehouden met het feıt dat slecnts een gedeelte van de kolk nymphaeıden bevat. De jaarlıjkse produktıe van de meest dominante nympnaeıde ın kolk D, *Nymphoides peltata*, kan uıt de lıteratuur gehaald worden: 0,55 kg C/m^2; ın kolk D ıs de jaarlıjkse netto produktıe van deze makrofyt dus 4,4 ton C. De fytoplankton produktıe ıs dus ongeveer 6 maal hoger op jaarbasıs dan dıe van *Nymphoides peltata*. Indıen *Nymphoides peltata* ın de gehele kolk voor zou komen was de jaarlıjkse produktıe van het fytoplankton nog altıjd 2,4 maal meer dan dıe van *Nymphoides peltata*.

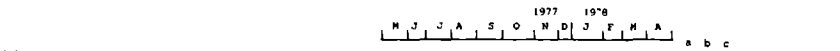
APPENDICES

Appendix Ia. Phytoplankton species in the samples taken from sampling locality F_1 (open water area) in pond F of the Oude Waal. Period: May 1977 to April 1978.

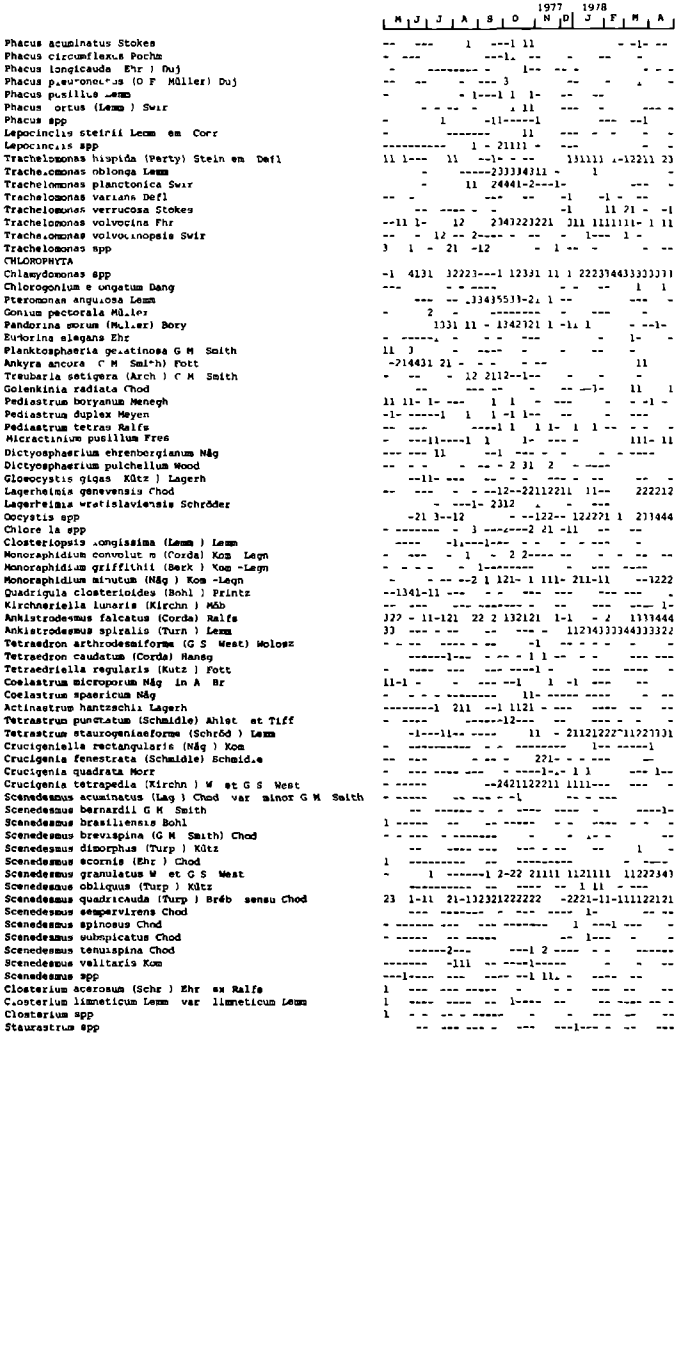
The abundance of the taxa is indicated as follows: 1 = occasional hit, 1-3 individuals per slide; 2 = 4-10 individuals; 3 = more than 10 individuals, not dominant; 4 = as 3, but dominant; 5 = mass occurrence.

Column a, b and c represent the frequency classes for the taxa; 1 = present in 1-20 % of the samples; 2 = in 21-40 %; 3 = 41-60 %; 4 = 61-80 %; 5 = 81-100%. Column a represents the entire period of investigation; column b: the period in which the aboveground biomass of the nymphaeids is present; column c: the period in which the aboveground biomass of the nymphaeids is absent.

	1977 1978 M J J A S O N D J F M A	a	b	c
CYANOBACTERIA				
Merismopedia tenuissima Lemm	- -- ----------2-.-----------1 ----------	1	1	.
Synechococcus leopoliensis (Racib Kom	----------2.2. ----------	1	0	.
Anabaena flos-aquae (Lyngb) Brēb	------44521- 1----------	1	2	.
Oscillatoria spp	--------212--12---1-----------11---- ----1---	1	2	.
Lyngbya limnetica Lemm	- ----2.2--12----------1 1 - --------	1	2	.
CHRYSOPHYTA				
Chrysococcus spp	1----------22--4444433322231345555554325555555	4	2	5
Kephyrion haemisphaericum (Lack) Conr	----------2-1213213212213	2	0	3
Kephyrion rubri-claustri Conr	-------4---2322---11---2112- ----------2	2	2	1
Kephyrion spirale (Lack) Conr	----------1--------11233222	1	0	2
Kephyrion tubiforme Fott	---------- ----------1123321--	.	0	2
Kephyrion/Pseudokephyrion spp	-------4---2322---.1---2112 ----------	2	2	1
Stenoxalyx moril fera G M Schmid	----------1----13312112-3221.---1	2	2	3
Stenoxalyx spp	--------- -- ----------11.----------	.	1	1
Uroglena volvox Ehr	-- ---------- 1 ----------	1	0	.
Dinobryon divergens Imhof	------4441..1.31-13-1---- ----1-1-------323324	3	3	2
Dinobryon spp	- - 2---1----------1---------- -------	1	1	1
Pseudokephyrion cylindricum Bourr	---------- ---1-----11212233	1	2	2
Pseudokephyrion entzii Conr	----------2221-111--1221132	2	2	3
Pseudokephyrion minutissimum Conr	----------33----------	1	0	1
Pseudokephyrion poculum Conr	- ----------111 1-31------	1	0	2
Mallomonas alveolata Perty em Iwanoff	-------221--1---1------1 - -111--1----1122222	2	2	3
Mallomonas tonsurata Teiling em Krieger	1------1122223 1 -1 11111	2	3	2
Mallomonas caudata Iwanoff in Krieger	----- 1 -2343422----1-11-1---1111.11--1 1-----	3	2	3
Mallomonas akrokomos Ruttner in Pascher	---244121-1----------1-----1 -2333333-.221111.1	3	2	4
Mallomonas spp	------1---.1.2----------1------2122222222222	3	2	4
Synura petersenii Korsh	2- - -----1---------11-----21-2313-.-3555542	2	1	4
Chrysophaerella spp	---------1112---------- ------- 111.111-	2	.	2
Chromophysomonas (Takahashi) Preisig et Hibberd	1------111111--------1--------1-1-1----.-1...141	2	2	3
Paraphysomonas spp	------2211--1---1----------1 122111121222.11.11	3	2	4
Bicoeca planktonica Kiss	- -- ----------1-1-1122332-11-1---------	2	0	3
XANTHOPHYTA				
Tetraedriella regularis (Kütz) Fott	----------1----------	1	0	1
Goniochloris mutica (A Br) Fott	1 - --------11-2234)112-2----1------ - .-1---	2	2	2
Goniochloris fallax Fott	----------1----- - ----------	1	1	0
Goniochloris smithii (Bourr) Fott	----------.----------	1	1	0
Ophiocytium capitatum Wolle	----------1-121----1----------	1	1	1
Tribonema spp	-------.---111---1------- - -- ----.----------	1	2	1
BACILLARIOPHYTA				
Aulacosira granulata (Ehr) Sim	-- ----2223532111333333322221----2--21 ---2---	3	4	3
Melosira varians Ag	-1------12221-----1-------- 1 ----------	1	2	1
Cyclotella comta (Ehr) Kütz.	--2311----------1----1---1---1-1----1---1---	1	.	1
Cyclotella kützingiana Thwaites	- ----------1----------	.	0	1
Cyclotella meneghiniana Kütz	111--1-1544444455554444444555554474321?-2344444	5	5	5
Cyclotella ocellata Pantocsek	----------1-2-----	1	0	1
Cyclotella pseudostelligera Hustedt	------1-----1----3321232222 - - ----------	2	2	2
Stephanodiscus astrea (Ehr) Grun	----------3----------2---	1	0	1
Stephanodiscus hantzschii Grun	---2 ---5-?2223-2323433333333343245555555552443	4	3	5
Diatoma elongatum (Lyngb) Ag	22221121----111--1112211---1 1221-.?2222333333	4	4	4
Diatoma vulgare Bory	----------.	1	0	1
Diatoma vulgare var ehrenbergii (Kütz) Grun	-- 1 -- - ----------1----------	1	1	?
Diatoma vulgare var producta Grun	---------- -----1------- .	.	0	1
Opephora martyi Héribaud	----------1----------11-- .	.	.	1
Fragilaria bidens Heiberg	----- 11111-1-1-1----------	1	2	0
Fragilaria brevistriata Grun	------1---------- ----------	1	1	0
Fragilaria capucina Desm	----------112----------11-----22122223-	2	4	2
Fragilaria capucina var mesolepta (Rab) Grun	-------1----------	1	4	0
Fragilaria construens (Ehr) Grun	----------1----------	1	0	1
Fragilaria construens var venter (Ehr) Grun	------1---------- ----------	1	1	0
Fragilaria crotonensis Kitton	-----111-1111--1-333334- -----1----------1222	3	3	2
Fragilaria vaucheriae Kütz	2--2--2-3 --12-1111-----2----12433333333231-3	3	3	4
Fragilaria virescens Ralfs	----------2------ -- -----	1	0	1
Synedra acus Kütz	1221--1-211222222333321---1-----1-----222-----2	3	5	2
Synedra parasitica (W Smith) Hustedt	------ - ----------	.	.	1
Synedra pulchella Ralfs Kütz	-2---1--1----------	1	.	0
Synedra tabulata Ag) Kütz var fasciculata(Kütz) Grun	-211.1111232221322----1----------	2	5	1
Synedra ulna (Nitzsch) Ehr	221111-12 - 112--12----------22-222123322233345	4	4	4
Synedra ulna var biceps (Kütz) Von Schönfeldt	- ----------1----------	1	0	1
Synedra spp	---2---------- ----------	1	1	0
Asterionella formosa Hassall	---321--1111321123-313413222222-222123322233345	5	4	5
Eunotia lunaris (Ehr) Grun.	---1---------- - -----1122-1-22-2	1	1	2
Cocconeis pediculus Ehr	-1-1111111222--222111-----1---121-1-2111-12--1	4	4	3
Cocconeis placentula Ehr	-1- -12-2232221222211-----1---11112-1---1---1---	3	4	2
Cocconeis scutellum Ehr var stauroneiformis W Smith	---------- - -1-- 11----------	1	0	1
Achnanthes conspicua A Mayer	----------1----------	1	0	.
Achnanthes hauckiana Grun	----------1 ----------.1---111-222-2-222	2	1	3
Achnanthes lanceolata (Brēb) Grun	-1---11-1-1---2-----1----------	1	2	1



	a	b	c
Achnanthes lanceolata f ventricosa Hustedt	1	1	0
Achnanthes linearis W Smith	1	1	0
Achnanthes microcephala (Kutz.) Grun	2	2	3
Rhoicosphenia abbreviata (Ag) Lange-B.	1	1	1
Frustulia vulgaris Thwaites	1	1	1
Navicula cincta (Ehr , Kutz	1	0	2
Navicula cryptocephala Kütz	4	3	4
Navicula cuspidata Kütz	1	1	0
Navicula exigua Greg) O Müller	1	0	.
Navicula gastrum Ehr	1	0	1
Navicula gracilis Ehr	1	2	1
Navicula gregaria Donkin	.	1	0
Navicula hungarica Grun	1	1	1
Navicula hungarica var capitata (Ehr) Cleve	1	1	1
Navicula lanceolata (Ag.) Kütz	1	1	1
Navicula menisculus Schumann	1	1	1
Navicula mutica Kütz	1	1	0
Navicula oblonga Kutz	1	0	1
Navicula peregrina (Ehr , Kütz	1	2	1
Navicula peregrina f minor Kolbe	1	1	1
Navicula protracta (Grun. Cleve	1	1	1
Navicula pupula Kütz.ng	1	1	1
Navicula pupula var rectangularis (Greg.) Grun.	1	1	0
Navicula radiosa Kütz	2	2	3
Navicula reinhardtii Grun	1	0	1
Navicula rhynchocephala Kütz	2	2	3
Navicula rotaeana (Rab) Grun	1	1	1
Navicula simplex Krasske	1	1	1
Navicula spp	1	1	0
Pinnularia microstauron (Ehr) Cleve	1	1	1
Pinnularia viridis (Nitzsch) Ehr.	1	0	1
Nedium iridis (Ehr) Cleve f vernalis Reichelt	1	0	1
Caloneis silicula (Ehr) Cleve	1	0	1
Gyrosigma acuminatum (Kütz) Rab	2	2	2
Amphora ovalis Kütz.	2	1	2
Cymbella affinis Kütz	1	0	1
Cymbella amphicephala Näg	1	1	1
Cymbella aspera (Ehr.) Cleve	1	1	0
Cymbella ehrenbergii Kütz	1	0	1
Cymbella microcephala Grun	1	1	1
Cymbella prostrata (Berkeley) Cleve	1	2	0
Cymbella cistula (Hempr) Grun.	1	1	1
Cymbella ventricosa Kutz.	2	2	2
Gomphonema acuminatum Ehr	1	1	1
Gomphonema acuminatum var coronata (Ehr) W Smith	1	1	1
Gomphonema constrictum Ehr	1	0	1
Gomphonema constrictum var. capitata (Ehr) Cleve	1	2	1
Gomphonema gracile (Ehr)	1	0	1
Goephonema olivaceum (Lyngb) Kütz	3	2	3
Gomphonema parvulum (Kütz) Grun.	2	1	2
Gomphonema spp	1	1	0
Epithemia sorex Kütz	1	0	1
Epithemia zebra (Ehr) Kütz	1	1	1
Hantzschia amphioxys (Ehr) Grun.	1	1	1
Nitzschia amphibia Grun.	1	1	0
Nitzschia diasipata (Kütz) Grun.	1	1	1
Nitzschia hungarica Grun	1	1	1
Nitzschia kützingiana Hilse	1	1	0
Nitzschia linearis W Smith	2	2	2
Nitzschia palea (Kütz) W Smith	3	4	3
Nitzschia pseudofonticola Hustedt	2	2	1
Nitzschia socialis Gregory	1	1	0
Cymatopleura elliptica (Bréb.) W Smith f nobilis (Hantzsch) Hustedt	1	1	0
Cymatopleura solea (Bréb.) W Smith	1	1	1
Surirella linearis W Smith	1	0	1
Surirella cf. tenera Gregory	1	1	0
Surirella ovata Kütz.	1	0	1
CRYPTOPHYTA			
Cryptomonas erosa Ehr.	4	3	5
Cryptomonas ovata Ehr	4	3	4
Cryptomonas spp	4	3	5
PYRRHOPHYTA			
Gymnodinium spp	3	1	4
Peridiniopsis sp	1	1	1
Peridinium spp.	4	2	5
Ceratium hirundinella (O F Müller) Schrank	1	2	1
EUGLENOPHYTA			
Euglena proxima Dang.	1	1	1
Euglena tripteris (Duj) Klebs	1	1	2
Euglena spp.	2	3	2

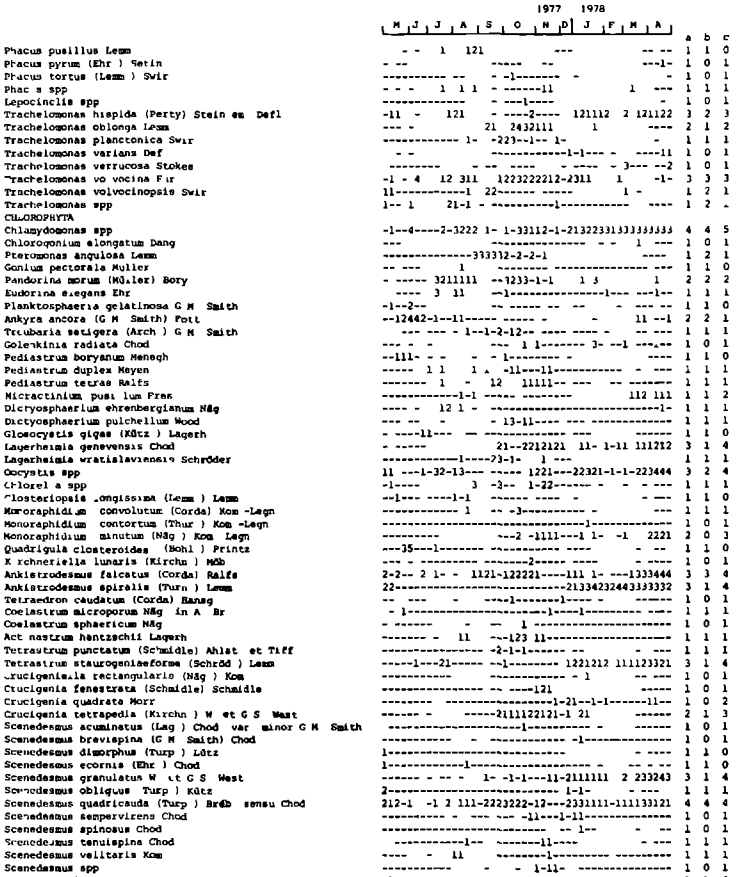

1977
1978
M J J A S O N D J F M A
a b c
Phacus acuminatus Stokes
Phacus circumflexus Pochm
Phacus longicauda Ehr) Duj
Phacus pseudonordstedtii (O F Müller) Duj
Phacus pusillus Lemm
Phacus ortus (Lemm) Swir
Phacus spp
Lepocinclis steinii Lemm em Corr
Lepocinclis spp
Trachelomonas hispida (Perty) Stein em Defl
Trachelomonas oblonga Lemm
Trachelomonas planctonica Swir
Trachelomonas varians Defl
Trachelomonas verrucosa Stokes
Trachelomonas volvocina Ehr
Trachelomonas volvocinopsis Swir
Trachelomonas spp
CHLOROPHYTA
Chlamydomonas spp
Chlorogonium euchlorum Ehr
Pteromonas angulosa Lemm
Gonium pectorale Müller
Pandorina morum (Müller) Bory
Eudorina elegans Ehr
Planktosphaeria gelatinosa G M Smith
Ankyra ancora G M Smith) Fott
Treubaria setigera (Arch) G M Smith
Golenkinia radiata Chod
Pediastrum boryanum Menegh
Pediastrum duplex Meyen
Pediastrum tetras Ralfs
Micractinium pusillum Fres
Dictyosphaerium ehrenbergianum Näg
Dictyosphaerium pulchellum Wood
Gloeocystis gigas Kütz) Lagerh
Lagerheimia genevensis Chod
Lagerheimia wratislaviensis Schröder
Oocystis spp
Chlorella spp
Closteriopsis longissima (Lemm) Lemm
Monoraphidium convolutum (Corda) Kom Legn
Monoraphidium griffithii (Berk) Kom -Legn
Monoraphidium minutum (Näg) Kom -Legn
Quadrigula closterioides (Bohl) Printz
Kirchneriella lunaris (Kirchn) Näb
Ankistrodesmus falcatus (Corda) Ralfs
Ankistrodesmus spiralis (Turn) Lemm
Tetraedron arthrodesmiforme (G S West) Wolosz
Tetraedron caudatum (Corda) Hansg
Tetraedriella regularis (Kutz) Fott
Coelastrum microporum Näg in A Br
Coelastrum sphaericum Näg
Actinastrum hantzschii Lagerh
Tetrastrum punctatum (Schmidle) Ahlst et Tiff
Tetrastrum staurogeniaeforme (Schröd) Lemm
Crucigeniella rectangularis (Näg) Kom
Crucigenia fenestrata (Schmidle) Schmidle
Crucigenia quadrata Morr
Crucigenia tetrapedia (Kirchn) W et G S West
Scenedesmus acuminatus (Lag) Chod var minor G M Smith
Scenedesmus bernardii G M Smith
Scenedesmus brasiliensis Bohl
Scenedesmus brevispina (G M Smith) Chod
Scenedesmus dimorphus (Turp) Kütz
Scenedesmus ecornis (Ehr) Chod
Scenedesmus granulatus W et G S West
Scenedesmus obliquus (Turp) Kütz
Scenedesmus quadricauda (Turp) Bréb sensu Chod
Scenedesmus sempervirens Chod
Scenedesmus spinosus Chod
Scenedesmus subspicatus Chod
Scenedesmus tenuispina Chod
Scenedesmus vellitaris Kom
Scenedesmus spp
Closterium acerosum (Schr) Ehr ex Ralfs
Closterium limneticum Lemm var limneticum Lemm
Closterium spp
Staurastrum spp

Appendix Ib. Phytoplankton species in the samples taken from sampling locality F_2 (nymphaeid-dominated area) in pond F of the Oude Waal. Period: May to April 1977.
The abundance of the taxa is indicated as follows: 1 = occasional hit, 1-3 individuals per slide; 2 = 4-10 individuals; 3 = more than 10 individuals, not dominant; 4 = as 3, but dominant; 5 = mass occurrence.
Column a, b and c represent the frequency classes for the taxa; 1 = present in 1-20 % of the samples; 2 = 21-40 %; 3 = 41-60 %; 4 = 61-80 %; 5 = 81-100 %. Column a represents the entire period of investigation; column b: the period in which the aboveground biomass of the nymphaeids is present; column c: the period in which the aboveground biomass of the nymphaeids is absent.

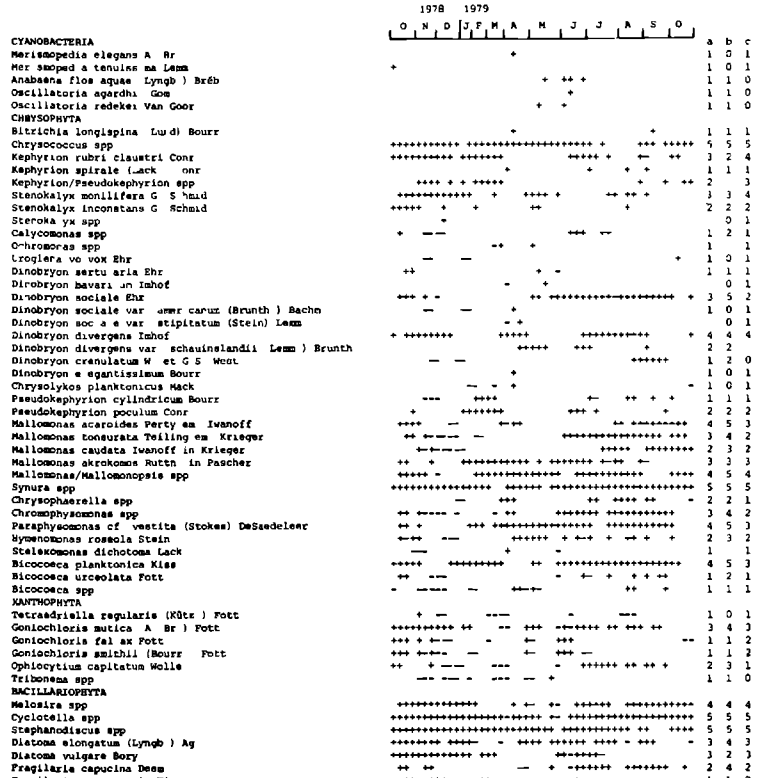
	1977 M	J	J	A	S	O	N	D	1978 J	F	M	A	a	b	c
CYANOBACTERIA															
Synechococcus leopoliensis (Racib.) Kom.							23						1	0	1
Anabaena flos-aquae (Lyngb.) Bréb.						45	421	11	42				1	2	1
Oscillatoria spp.						1	1	11	1				1	1	1
Lyngbya limnetica Lemm.							1	1	11		1	1	1	1	1
CHRYSOPHYTA															
Chrysococcus spp.						2	12	33	1333	221	2455554	12555555	4	2	5
Kephyrion haematopharicum (Lack.) Conr.									1	12	2	2323	2	0	3
Kephyrion rubri-claustri Conr.						2	3	3	2322				1	2	1
Kephyrion spirale (Lack.) Conr.											1	233	1	0	2
Kephyrion tubiforme Pott											1	223	1	0	2
Kephyrion/Pseudokephyrion spp.					2	1	32	1	1	21	1		1	2	1
Stenokalyx monilifera G.M. Schmid								3	1	1	1	1	2	0	2
Stenokalyx spp.											11		1	0	1
Uroglena volvox Ehr.											1		1	0	1
Dinobryon divergens Imhof					5	3	1	3	1	21	1	1	2	2	2
Dinobryon spp.							1	1	1	1	1		1	1	1
Pseudokephyrion cylindricum Bourr.											1	112	1	0	2
Pseudokephyrion entzii Conr.									2	111	112	1221	1	2	0
Pseudokephyrion minutissimum Conr.								33	2				1	0	1
Pseudokephyrion poculum Conr.									1	1	2	121	1	0	2
Mallomonas acaroides Perty em. Iwanoff					1	2	1	1	1	1	1	122	2	2	2
Mallomonas tonsurata Teiling em. Krieger						1	2	2	2	1			1	1	1
Mallomonas caudata Iwanoff in Krieger						1	2	3	4	3	2	2	1	1	1
Mallomonas akrokomos Ruttner in Pascher					1	3	4	2	1	1	1	1	2	3	2
Mallomonas spp.					1	1	1	2	2	2	2	2	2	2	2
Synura petersenii Korsh.					1	1	1	1	1	1	1	1	1	1	1
Chrysosphaerella spp.					1	1	1	1	1	1	1	1	1	1	1
Chromophysomonas spp.					1	1	1	1	1	1	1	1	1	1	1
Paraphysomonas spp.					1	1	1	1	1	1	1	1	1	1	1
Bicoeceа planktonica Kiss.								2	1	1	3	3	2	0	3
XANTHOPHYTA															
Gonichloris mutica (A. Br.) Pott					1	1	1	1	1	1	1	1	2	2	2
Ophiocytium capitatum Wolle								1	1				1	1	0
Tribonema spp.					1	1	1	1	1	1	1	1	1	1	1
BACILLARIOPHYTA															
Aulacosira granulata (Ehr.) Sim.					2	2	2	2	1	2	3	3	3	3	4
Melosira varians Ag.					1	3	3	3	2	1	1	1	1	1	1
Cyclotella comta (Ehr.) Kütz.					1	1	1	1	1	1	1	1	1	1	1
Cyclotella kützingiana Thwaites												1	1	0	1
Cyclotella meneghiniana Kütz.					1	1	1	1	1	1	1	1	1	1	1
Cyclotella pseudostelligera Hustedt									1	1	2	2	2	2	2
Stephanodiscus astrea (Ehr.) Grun.									1	1	2	2	1	0	1
Stephanodiscus hantzschii Grun.					1	1	1	1	2	2	2	2	1	1	1
Diatoma elongatum (Lyngb.) Ag.					1	1	1	1	1	1	1	1	1	1	1
Diatoma vulgare Bory													1	0	1
Diatoma vulgare var. producta Grun.													1	1	0
Fragilaria bidens Heiberg													1	1	0
Fragilaria capucina Desm.					1	1	1	1	1	1	1	1	1	1	1
Fragilaria capucina var. mesolepta (Rab.) Grun.													1	1	0
Fragilaria construens (Ehr.) Grun.													1	0	1
Fragilaria construens var. venter (Ehr.) Grun.													1	2	1
Fragilaria crotonensis Kitton													1	2	1
Fragilaria vaucheriae Kütz.													1	1	1
Synedra acus Kütz.													1	1	1
Synedra capitata Ehr.													1	0	1
Synedra parasitica (W. Smith) Hustedt var. subconstricta Grun.													1	0	1
Synedra pulchella (Ralfs) Kütz.													1	1	1
Synedra tabulata var. fasciculata (Kütz.) Grun.													2	2	1
Synedra ulna (Nitzsch) Ehr.													4	4	4
Synedra ulna var. biceps (Kütz.) Von Schönfeldt													1	1	0
Asterionella formosa Hassall													4	2	5
Eunotia lunaris (Ehr.) Grun.													2	1	1
Eunotia pectinalis (Dillwyn) Rab.													1	0	1
Cocconeis pediculus Ehr.													4	4	4
Cocconeis placentula Ehr.													4	5	3
Cocconeis scutellum Ehr.													1	1	1
Achnanthes hauckiana Grun.													2	0	3
Achnanthes lanceolata (Bréb.) Grun.													1	2	1
Achnanthes lanceolata f. rostrata (Ostrup) Hustedt													1	1	0
Achnanthes lanceolata f. ventricosa Hustedt													1	1	0
Achnanthes microcephala (Kütz.) Grun.													2	2	2
Rhoicosphenia abbreviata (Ag.) Lange-B.													1	1	1
Amphipleura pellucida Kütz.													1	1	0
Stauroneis phoenicenteron Ehr.													1	0	1

	1977 1978 M J J A S O N D J F M A	a	b	c
Stauroneis smithii Grun.	----------1----------	1	1	0
Navicula cincta (Ehr Kütz	------1----------2-222-1-212-2----	1	1	2
Navicula cryptocephala Kütz	2-11321112-2-1--1---1-----2--1------2112	3	4	2
Navicula cuspidata Kütz	----------	1	0	1
Navicula cuspidata var ambigua (Ehr) Cleve	------1----------	1	1	0
Navicula dicephala (Ehr) W Smith	------1----------	1	1	0
Navicula gracilis Ehr	--------1-1-1---1-1-111-1----------	2	2	1
Navicula hungarica Grun	--------1---1-1--1---1-1-111--22-12-1- 211----	2	1	3
Navicula hungarica var capitata (Ehr) Cleve	------1---------1----------	1	1	0
Navicula lanceolata Ag) Kütz	----------	1	0	1
Navicula menisculus Schumann	---------1-1-1-----1-1-1-1----------	1	1	1
Navicula muralis Kütz	------1----------	1	1	0
Navicula oblonga Kütz	--------- ----------2-1---2222----------	1	0	2
Navicula peregrina (Ehr) Kütz	----------1-1-------1----------	1	1	1
Navicula peregrina f minor Kolbe	----------1-------1-------1-----122-1-1---112----	2	1	2
Navicula protracta Grun) Cleve	------1-1--- ----------	1	1	0
Navicula pupula Kütz	--------1--------11---1---1--1- --- -- ------	1	1	1
Navicula pupula var rectangularis (Greg) Grun	----------1-------1----------	1	1	1
Navicula radiosa Kütz	--------1-1-- 1-1-1-1-1-1-1---3223--2-1-2211---	3	2	3
Navicula rhynchocephala Kütz	--------1-1---11-11-1-1-1-1---3-2221--2--2--2--	2	2	3
Navicula rotaeana (Rab) Grun	----------11----------	1	1	0
Navicula simplex Krasske	----------1----------	1	1	0
Navicula spp	---1--11----------1----------	1	1	1
Pinnularia microstauron (Ehr) Cleve	----------11----	1	0	1
Pinnularia viridis (Nitzsch) Ehr	----------1----------	1	0	1
Neidium dubium (Ehr) Cleve	----------1----------	1	0	1
Neidium iridis (Ehr) Cleve	----------1---------1----------	1	0	1
Neidium iridis f ventralis Reichelt	----------1----------	1	0	1
Caloneis silicula (Ehr) Cleve	----------1----.	1	0	1
Gyrosigma acuminatum (Kütz) Rab	----1---1-1---11-11-1-11.11--222121-----2-----	3	2	3
Amphora ovalis Kütz	--1---------1-12-11-1-1-1111--21---1-2--1-1----2	3	2	3
Amphora ovalis var pediculus Kütz	-----1----------	1	1	0
Cymbella amphicephala Näg	----1--1---------1----------	1	1	0
Cymbella aspera (Ehr) Cleve	--------111----1--------1----------	1	1	1
Cymbella ehrenbergii Kütz	--------1-1---------1----1--------	1	1	1
Cymbella lanceolata (Ehr) Van Heurck	----------1	1	0	1
Cymbella microcephala Grun	-------1---------11----------	1	1	1
Cymbella obtusiuscula (Kütz) Grun	----------1----------	1	0	1
Cymbella prostrata (Berkeley) Cleve	---1-22----1---------1----------	1	1	1
Cymbella tumida (Brēb.) Van Heurck	------1----------	1	1	0
Cymbella ventricosa Kütz	--11-1111-1---------1-------11-1---2-	2	2	1
Cymbella cistula (Hempr) Grun.	--------1-1-------1----------	1	1	1
Gomphonema olivaceum (Lyngb) Kütz.	-----22-2-1-2222---1-1-1---1----22-22-32333-22-	3	3	3
Gomphonema acuminatum Ehr	------1-----3212111111---1---1--2-----222--2---	2	3	2
Gomphonema acuminatum var. coronata (Ehr) W. Smith	----------1-1-3-21----------12--22-	1	2	1
Gomphonema constrictum Ehr.	----------212----1----------	1	0	1
Gomphonema constrictum var. capitata (Ehr) Cleve	------1-2-2-32232-1-1-----1----------1-----2	2	3	1
Gomphonema gracile Ehr	----------1----------	1	0	1
Gomphonema intricatum Kütz.	--------1-----1----------	1	1	0
Gomphonema parvulum (Kütz.) Grun.	-----111----------2-222-233232222	2	1	3
Gomphonema spp.	-------1----------	1	1	0
Epithemia sorex Kütz.	----------11---------1----------	1	1	1
Epithemia turgida (Ehr) Kütz	----------1--1-1-----1----------	1	1	1
Epithemia zebra (Ehr) Kütz.	---1----------	1	1	0
Epithemia zebra f porcellus (Kütz) Grun.	----------1----------	1	1	0
Rhopalodia gibba (Ehr) O F Müller	----------1--1-1----------	1	1	1
Rhopalodia gibba var ventricosa (Ehr) Grun.	----------1-------1----------	1	1	1
Hantzschia amphioxys (Ehr.) Grun.	----------3--1----1-1-1----1-----1-------	1	1	1
Nitzschia amphibia Grun.	-------2---2----------	1	1	0
Nitzschia dissipiata (Kütz.) Grun.	---1-11-1-112-12-11-1----------	2	3	1
Nitzschia hungarica Grun	---------1---------111-1-1----------	1	1	1
Nitzschia linearis W Smith	-1-------2-4-34332222333----------	2	3	1
Nitzschia palea (Kütz) W Smith	--212532311-2-1--322333-1-2----------	3	4	1
Nitzschia pseudofonticola Hustedt	------1-1-1-1-2323211-1-222----------1	2	3	2
Nitzschia sigma (Kütz) W Smith	----1----------	1	1	0
Cymatopleura elliptica (Brēb) W Smith	----------1---------1----------	1	0	1
Cymatopleura solea (Brēb) W Smith	--------1---1---------1-----21----------	1	1	1
Surirella linearis W Smith	----------1----------	1	1	0
Surirella ovata Kütz	----------2---2--1-	1	0	1
CRYPTOPHYTA				
Cryptomonas erosa Ehr	---32---1--2-123-11-2-2--2-32444444423333233221	4	3	5
Cryptomonas ovata Ehr.	--1-212-1--2-12-11-112-221----2333321-1-3-2211-	4	3	4
Cryptomonas spp	111----23-11-11-2-11-1---1232344444444.444332333	4	3	5
PYRRHOPHYTA				
Gymrodinium Stein spp.	------1----1------1------11-1-232113-323333322	3	1	4
Peridiniopsis Lemm	----------1----------	1	0	1
Peridinium spp.	----------2-21--14341111-1-21212-333233334	3	1	5
Ceratium hirundinella (O.F Müller) Schrank	----------1----------	1	1	0
EUGLENOPHYTA				
Euglena trapteris (Duj) Klebs	----------11----11----11----------1---	1	1	2
Euglena spp.	-----1111----12--------11-----1-11------1111-1	2	2	2
Phacus acuminatus Stokes	----------11----------	1	1	1
Phacus longicauda (Ehr) Duj	----------1----------	1	1	0
Phacus pleuronectus (O F. Müller) Duj	----------1---1----------	1	1	1

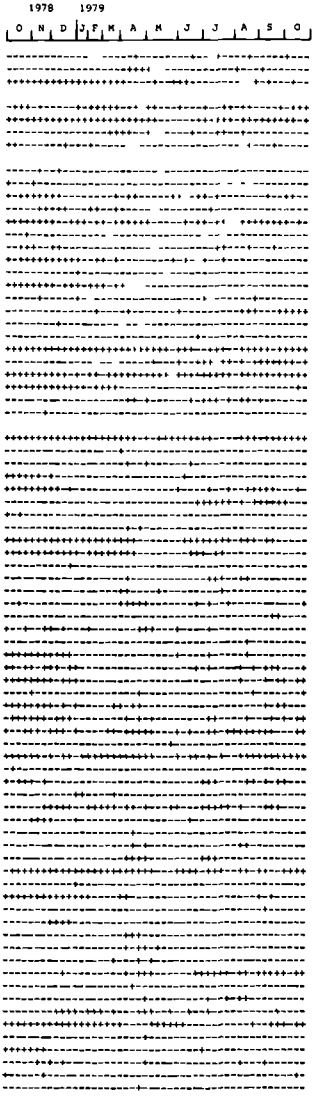
Appendix Ib. (continue)



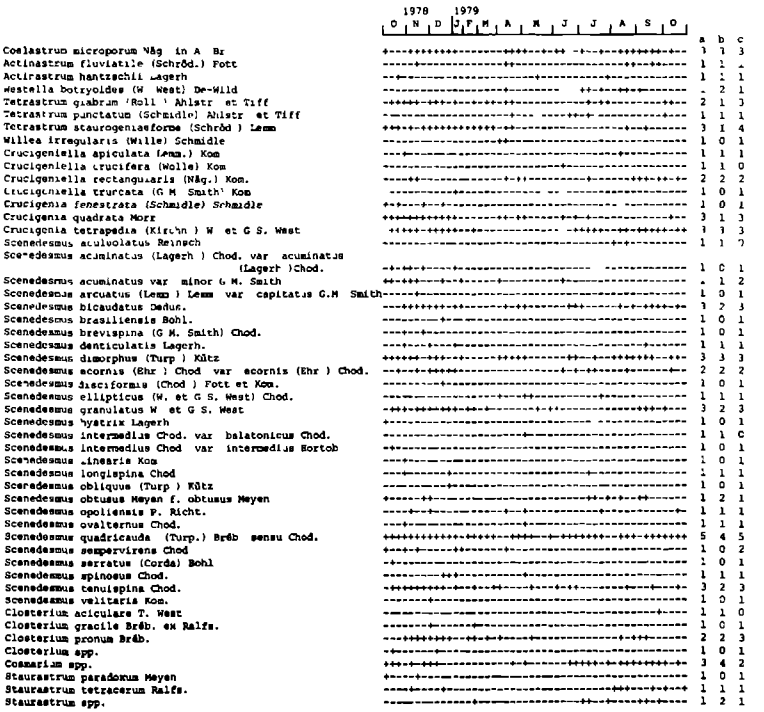
Appendix IIa. Phytoplankton species in the samples taken from sampling locality D_1 (open water area) in pond D of the Oude Waal. Period October 1978 to November 1979.
+ = present; - = absent.
The frequency classes of the taxa are indicated in columns a (entire investigation period), b (vegetation period of the nymphaeids) and c (the period in which the aboveground biomass of the nymphaeids was absent).
1 = present in 1-20 % of the samples; 2 = 21-40 %, 3 = 41-60 %; 4 = 61-80 %, 5 = 81-100 %.



	a	b	c
CYANOBACTERIA			
Merismopedia elegans A Br	1	0	1
Mer smoped a tenuiss ma Lemm	1	0	1
Anabaena flos aquae Lyngb) Bréb	1	1	0
Oscillatoria agardhi Gom	1	1	0
Oscillatoria redekei Van Goor	1	1	0
CHRYSOPHYTA			
Bitrichia longispina Luud) Bourr	1	1	1
Chrysococcus spp	5	5	5
Kephyrion rubri clsustri Conr	3	2	4
Kephyrion spirale (Lack onr	1	1	1
Kephyrion/Pseudokephyrion spp	2	3	
Stenokalyx monilifera G S hmid	3	3	4
Stenokalyx inconstans G Schmid	2	2	2
Steroka yx spp		0	1
Calycomonas spp	1	2	1
Chromoras spp	1		1
Croglera ve vox Ehr	1	0	1
Dinobryon sertu aria Ehr	1	1	1
Dinobryon bavari un Imhof		0	1
Dinobryon sociale Ehr	3	5	2
Dinobryon sociale var ames caruz (Brunth) Bache	1	0	1
Dinobryon soc a e var stipitatum (Stein) Lemm		0	1
Dinobryon divergens Imhof	4	4	4
Dinobryon divergens var schauinslandii Lemm) Brunth	2	2	
Dinobryon cranulatum W et G S West	1	2	0
Dinobryon e egantissimum Bourr	1	0	1
Chrysolykos planktonicus Mack	1	0	1
Pseudokephyrion cylindricum Bourr	1	1	1
Pseudokephyrion poculum Conr	2	2	2
Mallomonas acaroides Perty em Iwanoff	4	5	3
Mallomonas tonsurata Teiling em Krieger	3	4	2
Mallomonas caudata Iwanoff in Krieger	2	3	2
Mallomonas akrokomos Rutth in Pascher	3	3	3
Mallomonas/Mallomonopsis spp	4	5	4
Synura spp	5	5	5
Chrysophaerella spp	2	2	1
Chromophysomonas spp	3	4	2
Paraphysomonas cf vestita (Stokes) DeSaedeleer	4	5	3
Hymenomonas roseola Stein	2	3	2
Stelekomonas dichotoma Lack	1		1
Bicocoeca planktonica Kiss	4	5	3
Bicocoeca urceolata Pott	1	2	1
Bicocoeca spp	1	1	1
XANTHOPHYTA			
Tetraedriella regularis (Kütz) Pott	1	0	1
Goniochloris mutica A Br) Pott	3	4	3
Goniochloris fal ax Pott	1	1	2
Goniochloris smithii (Bourr Pott	1	1	2
Ophiocytium capitatum Wolle	2	3	1
Tribonema spp	1	1	0
BACILLARIOPHYTA			
Melosira spp	4	4	4
Cyclotella spp	5	5	5
Stephanodiscus spp	5	5	5
Diatoma elongatum (Lyngb) Ag	3	4	3
Diatoma vulgare Bory	3	2	3
Fragilaria capucina Desm	2	4	2
Fragilaria crotonensis Kitt	1	1	2
Fragilaria spp	1	2	1
Synedra acus Kütz	3	3	2
Synedra parasitica (W Smith) Husted var subconstricta Grun	1	1	1
Synedra ulna (Nitzsch) Ehr	3	2	3
Asterionella formosa Hass	4	3	5
Eunotia lunaris (Ehr) Grun	2	1	3
Cocconeis placentula Ehr	2	3	1
Cocconeis spp	2	1	3
Achnanthes spp	2	3	1
Rhoicosphenia abbreviata (Ag) Lange-B	2	2	3
Navicula cf cryptocephala Kütz	1	1	1
Navicula hungarica Grun	2	1	4
Navicula oblonga Kütz	1	0	2
Navicula peregrina Ehr Kütz f minor Kolbe	2	1	2
Navicula pupula Kütz	2	2	3
Navicula radiosa Kütz	3	3	4
Navicula rhynchocephala Kütz	2	1	3
Navicula spp	3	2	4
Pinnularia spp	1	0	1
Caloneis spp	1	1	2
Amphora spp	2	1	3
Cymbella spp	1	1	2
Gomphonema spp	3	3	4
Epithemia spp	2	0	3
Rhopalodia spp	1	0	1
Nitzschia/Hantzschia spp	5	5	4
Cymatopleura solea (Bréb) W Smith	1	0	2
Surirella spp	1	1	1



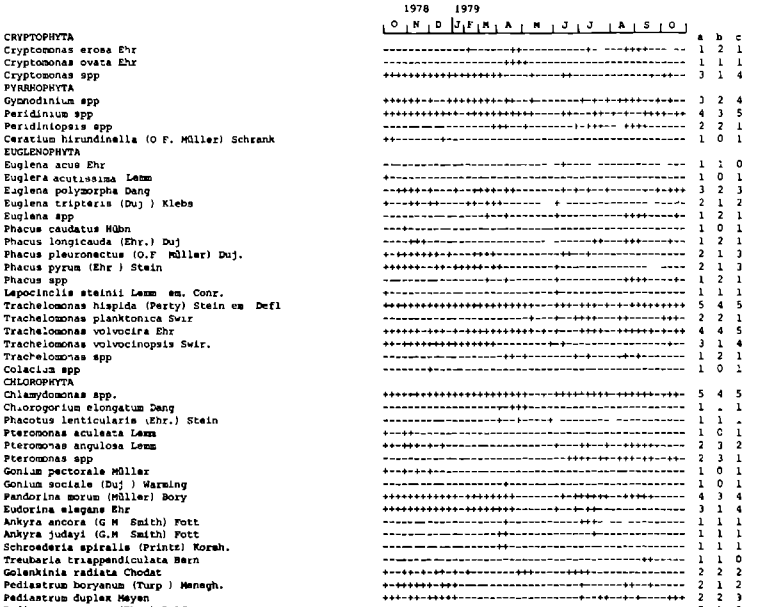
	a	b	c
CRYPTOPHYTA			
Cryptomonas erosa Ehr.	1	1	1
Cryptomonas ovata Ehr	1	1	1
Cryptomonas spp	3	2	4
PYRRHOPHYTA			
Gymnodinium spp.	3	2	3
Peridinium spp	5	4	5
Peridiniopsis spp	1	2	1
Ceratium hirundinella (O.F. Müller) Schrank	1	1	1
EUGLENOPHYTA			
Euglena acus Ehr.	1	0	1
Euglena acutissima Lemm	1	0	1
Euglena polymorpha Dang	2	2	3
Euglena tripteris (Duj) Klebs	2	1	2
Euglena spp	4	3	4
Phacus caudatus Hübn	1	0	1
Phacus longicauda (Ehr) Duj	1	1	1
Phacus pleuronectes (O F. Müller) Duj.	2	1	3
Phacus pusillus Lemm	1	0	1
Phacus pyrum (Ehr) Stein	2	0	3
Phacus triqueter (Ehr.) Duj.	1	1	1
Phacus spp	2	2	2
Lepocinclis steinii Lemm em Conr.	1	0	1
Trachelomonas caudata (Ehr) Stein	1	1	0
Trachelomonas hispida (Perty) Stein em. Defl.	5	4	5
Trachelomonas planktonica Swir	2	3	1
Trachelomonas volvocina Ehr	5	5	5
Trachelomonas volvocinopsis Swir.	2	0	4
Trachelomonas spp.	2	2	1
Colacium spp	1	1	1
CHLOROPHYTA			
Chlamydomonas spp.	5	4	5
Chlorogonium elongatum Dang	1	0	1
Phacotus lenticularis (Ehr.) Stein	1	1	1
Pteromonas aculeata Lemm	1	1	2
Pteromonas angulosa Lemm	2	2	3
Pteromonas spp.	2	3	1
Gonium pectorale Müller	1	0	1
Gonium sociale (Duj) Warming	1	0	1
Pandorina morum (Müller) Bory	4	3	4
Eudorina elegans (Ehr.)	3	2	4
Planktosphaeria gelatinosa G.M. Smith	1	0	1
Ankyra ancora (G M Smith) Fott	1	2	1
Ankyra judayi (G M. Smith) Fott	1	1	1
Schroederia spiralis (Printz) Korsh.	1	1	1
Treubaria triappendiculata Bern.	1	1	0
Golenkinia radiata Chodat	2	1	2
Pediastrum integrum Näg.	1	1	0
Pediastrum boryanum (Turp.) Menegh.	2	1	3
Pediastrum duplex Meyen	2	2	2
Pediastrum tetras (Ehr.) Ralfs	2	1	3
Micractinium crassisetum Hortob.	1	1	1
Micractinium pusillum Fres	2	1	3
Dictyosphaerium ehrenbergianum Näg.	2	2	3
Dictyosphaerium pulchellum Wood	3	4	3
Gloeocystis vesiculosa Näg.	1	1	0
Lagerheimia genevensis (Chod) Chod.	4	4	5
Lagerheimia longiseta (Lemm.) Wille	1	0	1
Lagerheimia wratislaviensis Schröd.	2	1	2
Oocystis lacustris Chod	1	0	1
Oocystis marssonii Lemm.	3	3	3
Chlorella spp	1	1	1
Chlorolobion braunii (Näg) Kom.	1	0	1
Closteriopsis longissima (Lemm.) Lemm	1	1	1
cf Monoraphidium arcuatum (Korsh) Hind	1	1	1
Monoraphidium contortum (Thur.) Kom -Legn	4	3	5
Monoraphidium griffithii (Berk.) Kom.-Legn	1	0	1
Monoraphidium minutum (Näg) Kom -Legn	2	1	3
Monoraphidium komarkovae Nyg	1	1	0
Kirchneriella contorta (Schmidle) Bohl	1	0	1
Kirchneriella contorta var elongata (G M. Smith) Kom	1	0	1
Kirchneriella irregularis (G M Smith) Korsh.	1	1	1
Kirchneriella lunaris (Kirch.) Moeb.	1	1	1
Kirchner ella obesa (W West) Schmidle	3	4	2
Kirchneriella subcapitata Korsh.	1	0	1
Quadrigula closterioides (Bohl) Printz	1	2	0
Quadrigula lacustris (Chod) G M Smith	2	2	2
Ankistrodesmus falcatus (Corda) Ralfs	5	2	5
Ank.strodesmus gracilis (Reinsch , Korsh	1	1	0
Tetraedron arthrodesmiforme (G.S. West) Wolosz	1	1	2
Tetraedron caudatum (Corda) Hanes	1	1	1
Tetraedron minimum (A Br) Hanes	1	0	1
Tetraedron incus (Telling) G.M Smith	1	0	1

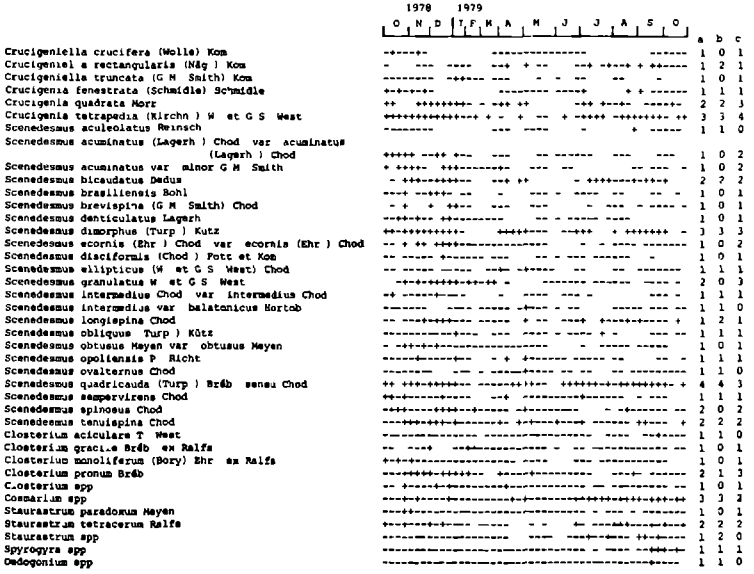

1978
1979
O N D J F M A M J J A S O
a b c
Coelastrum microporum Näg in A Br 3 1 3
Actinastrum fluviatile (Schröd.) Fott 1 1 1
Actinastrum hantzschii Lagerh 1 1 1
Westella botryoides (W West) De-Wild 2 1
Tetrastrum glabrum (Roll) Ahlstr et Tiff 2 1 3
Tetrastrum punctatum (Schmidle) Ahlstr et Tiff 1 1 1
Tetrastrum staurogeniaeforme (Schröd) Lemm 3 1 4
Willea irregularis (Wille) Schmidle 1 0 1
Crucigeniella apiculata (Lemm.) Kom 1 1 1
Crucigeniella crucifera (Wolle) Kom 1 1 0
Crucigeniella rectangularis (Näg.) Kom. 2 2 2
Crucigeniella truncata (G M Smith) Kom 1 0 1
Crucigenia fenestrata (Schmidle) Schmidle 1 0 1
Crucigenia quadrata Morr 3 1 3
Crucigenia tetrapedia (Kirchn) W et G S. West 3 3 3
Scenedesmus aculeolatus Reinsch 1 1 2
Scenedesmus acuminatus (Lagerh) Chod. var acuminatus (Lagerh)Chod. 1 0 1
Scenedesmus acuminatus var minor G M. Smith 1 1 2
Scenedesmus arcuatus (Lemm) Lemm var capitatus G.M Smith 1 0 1
Scenedesmus bicaudatus Dedus. 3 2 3
Scenedesmus brasiliensis Bohl. 1 0 1
Scenedesmus brevispina (G M. Smith) Chod. 1 0 1
Scenedesmus denticulatis Lagerh. 1 1 1
Scenedesmus dimorphus (Turp) Kütz 3 3 3
Scenedesmus acornis (Ehr) Chod var acornis (Ehr) Chod. 2 2 2
Scenedesmus disciformis (Chod) Fott et Kom. 1 0 1
Scenedesmus ellipticus (W. et G S. West) Chod. 1 1 1
Scenedesmus granulatus W et G S. West 3 2 3
Scenedesmus hystrix Lagerh 1 0 1
Scenedesmus intermedius Chod. var balatonicus Chod. 1 1 0
Scenedesmus intermedius Chod var intermedius Hortob 1 0 1
Scenedesmus linearis Kom 1 0 1
Scenedesmus longispina Chod 1 1 1
Scenedesmus obliquus (Turp) Kütz 1 0 1
Scenedesmus obtusus Meyen f. obtusus Meyen 1 2 1
Scenedesmus opoliensis P. Richt. 1 1 1
Scenedesmus ovalternus Chod. 1 1 1
Scenedesmus quadricauda (Turp.) Bréb sensu Chod. 5 4 5
Scenedesmus sempervirens Chod 1 0 2
Scenedesmus serratus (Corda) Bohl 1 0 1
Scenedesmus spinosus Chod. 1 1 1
Scenedesmus tenuispina Chod. 3 2 3
Scenedesmus velitaris Kom. 1 0 1
Closterium aciculare T. West 1 1 0
Closterium gracile Bréb. ex Ralfs. 1 0 1
Closterium pronum Bréb. 2 2 3
Closterium spp. 1 0 1
Cosmarium spp. 3 4 2
Staurastrum paradoxum Meyen 1 0 1
Staurastrum tetracerum Ralfs. 1 1 1
Staurastrum spp. 1 2 1

Appendix IIb. Phytoplankton species in the samples taken from sampling locality D_2 (nymphaeid-dominated area) in pond D of the Oude Waal. Period: October 1978 to November 1979.
The frequency classes of the taxa are indicated in columns a (entire investigation period), b (vegetation period of the nymphaeids) and c (the period in which the aboveground biomass of the nymphaeids was absent).
1 = present in 1-20 % of the samples; 2 = 21-40 %; 3 = 41-60 %; 4 = 61-80 %; 5 = 81-100 %.

	a	b	c
CYANOBACTERIA			
Merismopedia elegans A Br	1	0	1
Merismopedia tenuissima Lemm	1	0	1
Anabaena flos-aquae (Lyngb) Bréb	1	1	1
Oscillatoria redekei Van Goor	1	1	0
CHRYSOPHYTA			
Bitrichia longispina (Lund) Bourr	1	2	1
Chrysococcus spp	5	5	5
Kephyrion rubri-claustri Conr	3	2	1
Kephyrion spirale (Lack) Conr	1	0	1
Kephyrion/Pseudokephyrion spp	2	1	3
Stenokalyx monilifera G Schmid	1	2	4
Stenokalyx inconstans G Schmid	2	2	2
Stenokalyx spp	1	0	1
Calycomonas spp	1	2	1
Ochromonas spp	1	1	0
Uroglena vo vox Ehr	1	0	1
Dinobryon sertularia Ehr	1	1	4
Dinobryon sociale Ehr	3	5	2
Dinobryon sociale var americanum (Brunth) Bachm	1	1	1
Dinobryon sociale var stipitatum (Stein) Lemm	1	0	1
Dinobryon divergens Imhof	4	4	4
Dinobryon divergens var schauinslandii (Lemm) Brunth	1	2	1
Dinobryon cremulatum W et G S West	2	2	0
Chrysolykos planktonicus Pack	1	0	1
Pseudokephyrion cylindricum Bourr	1	1	1
Pseudokephyrion poculum Conr	2	2	2
Mallomonas acaroides Perty em Iwanoff	4	4	3
Mallomonas tonsurata Teiling em Krieger	3	4	2
Mallomonas caudata Iwanoff in Krieger	2	3	2
Mallomonas akrokomos Ruttner in Pascher	3	3	3
Mallomonas/Mallomonopsis spp	4	5	3
Synura spp	5	5	5
Chrysosphaerella spp	1	2	1
Chromophyxomonas spp	2	4	1
Paraphysomonas cf vestita (Stokes) DeSaedeleer	4	4	3
Hymenomonas roseola Stein	2	3	2
Hymenomonas sp	1	0	1
Stelexomonas dichotoma Lack	1	0	1
Bicoecoeca planktonica Kiss	4	5	3
Bicoecoeca urceolata Pott	2	2	1
Bicoecoeca spp	1	2	1
XANTHOPHYTA			
Tetraedriella regularis (Kütz) Pott	1	0	1
Goniochloris mutica (A Br) Pott	3	3	3
Goniochloris fallax Pott	2	1	2
Goniochloris smithii (Bourr) Pott	2	1	2
Ophiocytium capitatum Wolle	2	2	1
Tribonema spp	1	1	0
BACILLARIOPHYTA			
Melosira spp	3	4	2
Cyclotella spp	5	5	5
Stephanodiscus spp	5	5	5
Diatoma elongatum (Lyngb) Ag	3	3	3
Diatoma vulgare Bory	3	2	4
Fragilaria capucina Desm	3	4	2
Fragilaria crotonensis Kitt	1	0	1
Fragilaria spp	2	3	1
Synedra acus Kutz	2	2	2
Synedra parasitica (W Smith) Husted var subconstricta Grun	4	1	0
Synedra ulna (Nitzsch) Ehr	3	3	4
Asterionella formosa Hass	4	3	4
Eunotia lunaris (Ehr) Grun	3	2	3
Eunotia pectinalis (Dillw) Rabenh	1	1	1
Cocconeis placentula Ehr	2	3	1
Cocconeis spp	2	1	4
Achnanthes spp	2	2	2
Rhoicosphenia abbreviata (Ag) Lange-B	2	1	3
Navicula cf cryptocephala Kütz	2	3	1
Navicula hungarica Grun	3	2	4
Navicula oblonga Kütz	1	0	2
Navicula peregrina (Ehr) Kütz f minor Kolbe	2	0	1
Navicula pupula Kütz	2	1	2
Navicula radiosa Kütz	4	3	4
Navicula rhynchocephala Kütz	3	2	4
Navicula spp	5	4	5
Pinnularia spp	1	1	1
Caloneis spp	1	0	1
Amphora spp	3	2	3
Cymbella spp	3	2	3
Gomphonema spp	3	2	2
Epithemia spp	2	1	3
Rhopalodia spp	1	1	1
Nitzschia/Hantzschia spp	5	5	4
Cymatopleura solea (Bréb) W Smith	1	1	2
Surirella spp	1	1	1

Appendix IIb. (continue)





	a	b	c
Crucigeniella crucifera (Wolle) Kom	1	0	1
Crucigeniel a rectangularis (Näg) Kom	1	2	1
Crucigeniella truncata (G M Smith) Kom	1	0	1
Crucigenia fenestrata (Schmidle) Sc'midle	1	1	1
Crucigenia quadrata Morr	2	2	3
Crucigenia tetrapedia (Kirchn) W et G S West	3	3	4
Scenedesmus aculeolatus Reinsch	1	1	0
Scenedesmus acuminatus (Lagerh) Chod var acuminatus (Lagerh) Chod	1	0	2
Scenedesmus acuminatus var minor G M Smith	1	0	2
Scenedesmus bicaudatus Dedus	2	2	2
Scenedesmus brasiliensis Bohl	1	0	1
Scenedesmus brevispina (G M Smith) Chod	1	0	1
Scenedesmus denticulatus Lagerh	1	0	1
Scenedesmus dimorphus (Turp) Kutz	3	3	3
Scenedesmus ecornis (Ehr) Chod var ecornis (Ehr) Chod	1	0	2
Scenedesmus disciformis (Chod) Fott et Kom	1	0	1
Scenedesmus ellipticus (W et G S West) Chod	1	1	1
Scenedesmus granulatus W et G S West	2	0	3
Scenedesmus intermedius Chod var intermedius Chod	1	1	1
Scenedesmus intermedius var balatonicus Hortob	1	1	0
Scenedesmus longispina Chod	1	2	1
Scenedesmus obliquus Turp) Kütz	1	1	1
Scenedesmus obtusus Meyen var obtusus Meyen	1	0	1
Scenedesmus opoliensis P Richt	1	1	1
Scenedesmus ovalternus Chod	1	1	0
Scenedesmus quadricauda (Turp) Bréb sensu Chod	4	4	3
Scenedesmus sempervirens Chod	1	1	1
Scenedesmus spinosus Chod	2	0	2
Scenedesmus tenuispina Chod	2	2	2
Closterium aciculare T West	1	1	0
Closterium gracile Bréb ex Ralfs	1	0	1
Closterium moniliferum (Bory) Ehr ex Ralfs	1	0	1
Closterium pronum Bréb	2	1	3
Closterium spp	1	0	1
Cosmarium spp	3	3	2
Staurastrum paradoxum Meyen	1	0	1
Staurastrum tetracerum Ralfs	2	2	2
Staurastrum spp	1	2	0
Spyrogyra spp	1	1	1
Oedogonium spp	1	1	0

Appendix IIIa. The taxonomical arrangement of the Chrysophyte and Prymnesiophyte taxa encountered in samples from pond D of the Oude Waal (October 1978 - November 1979).

Phylum CHRYSOPHYTA

Class CHRYSOPHYCEAE

subclass ACONTHOCHRYSOPHYCIDAE

Order RHIZOCHRYSIDALES

Family Stylococcaceae *Bitrichia*

subclass HETEROCHRYSOPHYCIDAE

Order CHROMULINALES

Family Chrysococcaceae *Chrysococcus Kephyrion Stenokalyx Calycomonas*

Order OCHROMONADALES

Family Ochromonadaceae *Ochromonas Uroglena*

Family Bicocoecaceae *Bicocoeca*

Family Dinobryaceae *Dinobryon Chrysolykos Pseudokephyrion*

Family Paraphysomonadaceae *Chromophysomonas Polylepidomonas Chrysosphaerella Paraphysomonas*

Family Mallomonadaceae *Mallomonopsis Mallomonas Synura*

subclass CRASPEDOMONADOPHYCIDAE

Order MONOSIGALES

Family Salpingoecaceae *Stelexomonas*

Phylum PRYMNESIOPHYTA (= HAPTOPHYTA)

Class PRYMNESIOPHYCEAE (= HAPTOPHYCEAE)

Order PRYMNESIALES

Family Coccolithophoraceae *Hymenomonas*

Appendix IIIb. Taxonomical arrangement of the Bacillariophyte taxa (Diatoms) encountered in samples from pond D of the Oude Waal (October 1978 to November 1979).

Phylum BACILLARIOPHYTA

Class BACILLARIOPHYCEAE

subclass EUPODISCOPHYCIDAE

Order MELOSIRALES *Melosira*

Order THALASSIOSIRALES *Aulacosira Cyclotella Stephanodiscus*

Order CHAETOCERALES *Acanthoceras*

subclass FRAGILARIOPHYCIDAE

Order FRAGILARIALES *Asterionella Diatoma Fragilaria Opephora Synedra*

Order TABELLARIALES *Tabellaria*

subclass NAVICULOPHYCIDAE

Order EUNOTIALES *Eunotia*

Order ACHNANTHALES *Achnanthes Cocconeis*

Order NAVICULALES *Caloneis Cymbella Diploneis Frustulia Gomphoneis Gomphonema Gyrosigma Navicula Neidium Pinnularia Rhoicosphenia*

Order EPITHEMIALES *Epithemia Rhopalodia*

Order NITZSCHIALES *Hantzschia Nitzschia*

Order SURIRELLALES *Surirella Cymatopleura*

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Curriculum vitae

Rudi Roijackers werd op 8 februari 1951 geboren te St. Willebrord (gem. Rucphen). Als telg uit een onderwijzersfamilie wilde ook hij al snel die richting in. Gekoppeld aan een snel groeiende belangstelling voor de biologie moest dat wel resulteren in een opleiding tot leraar biologie.

Daartoe werd na de lagere school besloten tot het volgen van een H.B.S.-b opleiding en wel aan de Newman-H.B.S. te Breda. In 1969 werd het einddiploma behaald en werd een aanvang gemaakt met de studie biologie aan de Katholieke Universiteit te Nijmegen. Het kandidaatsexamen werd aan deze universiteit behaald op 6 maart 1973 in de studierichting Big.

De doktoraalstudie biologie omvatte de volgende onderdelen:

- hoofdvak Aquatische Oecologie bij Prof. Dr. C. den Hartog: "Een vergelijkend hydrobiologisch onderzoek in een schone en een verontreinigde laaglandbeek" met accenten op de makrofauna en benthische diatomeeën, onder de directe leiding van mw. Dr. J.F.M. Geelen;
- bijvak Geobotanie bij Prof. Dr. V. Westhoff: "Minimumareaalonderzoek in enkele Nederlandse vegetatietypen", onder de directe leiding van Prof. Dr. E. van der Maarel en Prof. Dr. M.J.A. Werger;
- bijvak Didaktiek van de Biologie bij drs. R.M.L.A. Dolné, waarin een op een enquête gebaseerde inventarisatie werd verricht naar de omvang, inhoud en inrichting van de praktika biologie op de middelbare scholen in Nederland. Daaropvolgend is een onderzoek verricht naar de mogelijkheden voor een aquatisch oecologisch projekt voor de bovenbouw van HAVO en VWO.

Het doktoraalexamen Biologie werd op 2 december 1975 cum laude afgelegd; ook de onderwijsbevoegdheden werden op die dag verkregen.

Het middelbaar onderwijs had echter niet meer diezelfde aantrekkingskracht als voorheen, zeker vergeleken met het universitair onderwijs.

Het was daarom een fortuinlijk feit dat de tijdelijke benoeming van februari 1976 tot januari 1980 als wetenschappelijk medewerker bij het Laboratorium voor Aquatische Oecologie van de Katholieke Universiteit te Nijmegen, een grote onderwijsbelasting inhield.

In deze periode werd onder leiding van Prof. Dr. C. den Hartog een promotie-onderzoek verricht naar het fytoplankton in de Oude Waal, waarvan een deel van de resultaten in dit proefschrift is verwerkt.

Vanaf januari 1980 is hij lid van de vaste staf van de sektie Hydrobiologie aan de Landbouwhogeschool te Wageningen, alwaar zijn onderzoeksaktiviteiten zich concentreren op de oppervlaktewaterkwaliteit met als primaire ingang het fytoplankton.

Stellingen bij het proefschrift van R.M.M. Roijackers

I

De ontwikkeling van het fytoplankton in voor veldwerk minder aantrekkelijke jaargetijden is zowel kwalitatief als kwantitatief zeer belangrijk.

Dit proefschrift.

II

Het belang van het nanno- en het ultrafytoplankton qua soortensamenstelling, biomassa en produktiviteit wordt nog sterk onderschat.

Dit proefschrift.

III

Van de tot nu toe beschreven soorten binnen het Heliozoa-geslacht *Pinaciophora* is slechts de type-soort *P. fluviatilis* als zodanig te handhaven; op grond van de ultrastruktuur van schubben en stekels dient de soort *P. stammeri* ondergebracht te worden in het geslacht *Pompholyxophrys*, terwijl de overige soorten beter in het geslacht *Rabdiophrys* ondergebracht kunnen worden.

Siemensma, F., 1981. *De Nederlandse Zonnediertjes (Actinopoda, Heliozoa)*. Wetenschappelijke Mededelingen K.N.N.V., nr. 149: 118 pp.

Thomsen, H.A., 1978. On the identity between the heliozoan *Pinaciophora fluviatilis* and *Potamodiscus kalbei*; with the description of eight new *Pinaciophora* species. *Protistologica*, 14 359-373.

IV

Er zijn voldoende argumenten om het Heliozoa-geslacht *Acanthocystis* te splitsen in de door Durrschmidt aangeduide vier groepen.

Durrschmidt, M., 1985. Electron microscope observations on scales of species of the genus *Acanthocystis* (Centrohelida, Heliozoa) from Chile, I. *Arch. Protistenk.*, 129. 55-87.

V

Een goede 'lumper' moet wel bewezen hebben een goede 'splitter' te zijn.

VI

Zo lang de biologische waterbeoordeling niet integraal uitgevoerd wordt en het gehele ecosysteem met al zijn komponenten omvat, zal het op deze beoordeling gestaafde beheer niet veel verder komen dan die maatregelen die ook al zonder de genoemde beoordeling genomen worden.

VII

Gezien de toenemende druk op de studenten om de begonnen studie in een steeds korter wordende periode af te ronden, lijkt het verstandig de term *universiteit* te vervangen door *hogeschool*.

VIII

'..... in Italy for 30 years under the Borgia's they had warfare, terror, murder, bloodshed, but they produced Michaelangelo, Leonardo da Vinci and the Renaissance, and Switzerland, they had brotherly loved, they had 500 years of democracy and peace and what did that produce?... the cuckooclock'.....'

Harry Lime in de film *The third man* van Carol Reed (1949).

IX

Het verenigen van de Bacteria en de Cyanophyta in het fylum Cyanobacteria is niet alleen zinvol gezien hun systematische verwantschap, maar bovendien ook gezien hun ecologische verwantschap.

X

De vriendelijkste politiek is vriendjespolitiek.